# THE AERATION OF SLASH PINE ROOT SYSTEMS IN SATURATED SOILS

By

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For David and Yvonne Fisher

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Massive taproots and sinker roots of slash pine extend into zones of permanently saturated soil and appear undamaged by anoxia when submerged by periodic risings of the water table. This research addressed a general hypothesis that gaseous exchange through the wood of large-diameter roots supplied $O_2$ to the submerged ends of the root system and thus sustained aerobic functions.

Green wood of large-diameter sinkers and a taproot had unusually high air contents (48 to 63% of green volume), a consequence of low wood substance and low moisture volumes. Under small pressures, 0.06 to 0.98 kPa, air moved through air-spaces in root sections at least 40 cm long. Linear relationships between pressure gradient and outflow allowed the use of a Darcy K value to characterize air permeability, yielding a mean K of 74 $cm^2\ kPa^{-1}\ min^{-1}$. Air conduction was

distributed throughout the root cross-section, through connected air-filled tracheids. Thus, roots appeared simultaneously to conduct water up from, and air down to, submerged distal ends.

Iron oxides were precipitated on small live roots of slash pine seedlings grown in saturated anaerobic peat for at least 18 months, and Fe oxide-cemented rinds encrusted large-diameter sinkers and fine lateral roots of large trees in anaerobic subsoil. Local accumulations of Fe on live, oxidizing roots were from 4 to 96 times the concentrations in the reduced matrix of peat or soil and varied from <0.5 to 11.3 g Fe $cm^{-2}$ of root surface area.

Taproot systems of slash pine seedlings developed in solution cultures with near zero $O_2$ availability. These root systems actively absorbed K from $N_2$-sparged micro-aerobic solutions (0.5 ppm $O_2$) but exhibited sensitivity to the composition of gas surrounding unsubmerged portions of the basal taproot and stem. Treatments changing air for $N_2$ produced immediate, large K-effluxes from the roots in micro-aerobic solutions, which reversed to K-uptake when air replaced $N_2$. Solution roots were responding directly to fluctuations in $O_2$ transported from the basal taproot and stem region.

CHAPTER 1
GENERAL INTRODUCTION

## Slash Pine

Slash pine (Pinus elliottii Engelm. var. elliottii) grows naturally in low-relief landscapes affected by shallow water tables. On these sites, surface ponding occurs periodically, and subsoil is normally, if not constantly, saturated (Penfound, 1952; Schultz, 1973; Hebb and Clewell, 1976). Relatively shallow water-table levels benefit slash pine growth if surface soil saturation is infrequent, of short duration, or ameliorated by drainage (Barnes and Reiston, 1955; White and Pritchett, 1970; Kaufmann et al., 1977).

Slash pine develops a massive taproot that is commonly replaced at depth by large-diameter sinker roots. These vertical roots extend well below the highest water-table level (Fisher, 1983) and in the order of 1 m below the seasonally low water-table level (Schultz, 1972 and 1973). During prolonged periods of saturation, the soil $O_2$ is depleted and roots receiving no other supply of $O_2$ would eventually die (Crawford, 1978). Thus, it is improbable that the central taproot system of slash pine simply endures months or years of anoxia between periodic lowerings of the water table.

## Internal Aeration of Roots

Wetland plants have developed various mechanisms for coping with the lack of $O_2$ in soil (Armstrong and Boatman, 1967; Green and Etherington, 1977) and among these the provision of a ventilated root system is common to most species (Armstrong, 1982). In non-woody tissues of herbaceous and shrubby plants, intercellular space is increased in volume and continuity by separation and degradation of cell walls. The resulting aerenchymous tissue, usually in the primary cortex of stem and root, provides a connected, air-filled pore space that allows the exchange of gas between atmosphere and submerged root tissue. Adventitious roots with such structure grow in response to sudden flooding, often emerging from lenticels on woody stems or roots (Hook et al., 1970).

The development of secondary thickening with loss of the primary cortex poses a difficulty for large woody plants. Armstrong (1982) suggested that, in mature plants, the most obvious route for gaseous exchange is through empty conducting vessels in the stele. Extensive zones of gas-filled xylem elements occur in both angiosperms and gymnosperms, and can be shown experimentally to conduct gases (Coutts and Armstrong, 1976). A gas-conducting pathway, continuous with the atmosphere, connects air space in lenticels with intercellular space in phloem rays, across the cambium, and into xylem rays (Hook et al., 1972). It is

not yet clear, however, how radial and longitudinal pathways in xylem interconnect (Coutts and Armstrong, 1976)

Some species of relatively flood-tolerant pines seem to fit a model of xylem gas conduction. Flood-conditioned roots of lodgepole pine (Pinus contorta [Douglas ex Loudon]) seedlings and rooted cuttings are internally aerated, as indicated by rhizosphere oxidation (Phillipson and Coutts, 1978). Conditioned non-woody roots have longitudinally continuous air-filled lacunae within the primary stele. The lacunae extend from behind the root apex until closed by the growth of secondary xylem (Coutts and Armstrong, 1976). This gas-conducting pathway was shown to be continuous with lenticels on the root surface. Flood-conditioned roots of loblolly pine (Pinus taeda L.) and pond pine (Pinus serotina Michx.) form similar lacunate steles (Topa and McLeod, 1986b; Hook et al., 1988). The secondary xylem of lodgepole pine roots is also gas-conducting (Phillipson and Coutts, 1980). In woody lateral roots, bands of embolized latewood tracheids apparently conducted air longitudinally through root sections up to 45 cm in length, and radially to lenticels in the root periderm.

## Some Consequences of Internal Aeration of Roots

### Iron Oxide Accumulation on Roots

Iron oxide precipitation on roots growing in saturated reduced soil is an indication of $O_2$ release from the roots into the rhizosphere (Armstrong, 1968, 1982; Armstrong and

Boatman, 1967) and, accordingly, an indication of an internally transported supply of $O_2$ from the atmosphere to the deep oxidizing roots. Reports of Fe oxide precipitation on roots of trees are primarily limited to wetland species (Dickson and Broyer, 1972) but have also been observed on roots of mesophytic pines (Levan and Rhie, 1986; McKevlin et al., 1987). Presence of Fe oxide precipitates on the submerged root systems of slash pine have not been reported, but should be expected in certain reduced soil conditions if these roots are internally aerated.

Nutrient and Water Absorption

Root absorbing functions are disrupted by the lack of $O_2$ in soil, with the result that reduced transpiration is one of the first obvious effects of flooding on an unadapted root system (Armstrong, 1982). Active uptake of nutrients depends on high energy potentials provided by aerobic respiration within root tissues (Mengel, 1974; Clarkson, 1984). The absorption of K is particularly sensitive to cell respiration, yielding measurable changes in K-uptake or K-efflux with changes in $O_2$ supply to root systems (Rosen and Carlson, 1984). Thus the active uptake of K by roots in anaerobic or low-$O_2$ conditions is evidence of an internal mechanism of $O_2$ transport from atmosphere to the absorbing roots.

Experiments

The following research addresses the general hypothesis that gaseous exchange through the wood of large-diameter

roots supplies $O_2$ to submerged ends of the slash pine central root system and thus sustains aerobic root functions. Each of the three following chapters is a independent manuscript relating to a separate aspect of the general hypothesis and intended for journal publication.

Chapter 2 addresses a specific hypothesis, that the primary pathway for long-distance $O_2$ conduction, from atmosphere to deep distal root tips, is through the wood of large-diameter taproots or sinkers.

In Chapter 3, the presence of Fe oxide precipitates on deep roots of large slash pine trees and on the submerged taproot systems of cultivated slash pine saplings is investigated as evidence of rhizosphere oxidation.

Chapter 4 is a study of K-uptake by submerged taproot systems of slash pine saplings and of the sensitivity of K-uptake from micro-aerobic solutions to $O_2$ transported internally down from the basal taproot or stem above the saturated zone.

## CHAPTER 2
## AIR-CONDUCTING POROSITY IN SLASH PINE ROOTS

### Introduction

Slash pine (*Pinus elliottii* Engelm var. *elliottii*) grows naturally on the Atlantic and Gulf coastal plains of the southeastern United States, occupying shallow, peaty, fresh-water swamps (Penfound, 1952; Hebb and Clewell, 1976), as well as wet places by stream edges, pond margins and depressions in the flatwoods pinelands (Schultz, 1973). The species is now planted extensively throughout the region, and its growth is largely affected by water availability in the rooting zone (Barnes and Ralston, 1955; Kaufman, 1968). On these infertile, sandy soils, relatively shallow ground water levels benefit tree growth (White and Pritchett, 1970; Kaufman et al., 1977), although the basal stems and surface lateral roots should not be continually submerged (Pritchett and Smith, 1974). The taproot and second-order sinker roots of slash pine generally extend well below the highest water-table level (Fisher, 1983). Apparently normal, massive taproots and sinkers occur as much as 2 m below the short-term high water level and 0.9 m below the seasonally low level (Schultz, 1972 and 1973).

It seems improbable that the deep root systems simply endure protracted periods of anoxia. Absence of oxygen in

eventually fatal to all higher plant tissues (Crawford, 1978) and yet, on many soils, the deep distal parts of slash pine central root systems are submerged for several months or even a few years between periodic loweringa of the water table. Furthermore, primary and secondary root growth, uptake and transport functions require aerobic catabolic processes (Coutts, 1982; Hook, 1984, Jackson and Drew, 1984).

An internal gas-exchange mechanism between the atmosphere and oxygen-depleted tissues maintains the aerobic functions of some flooded root systems (Carpenter and Mitchell, 1980; Hook, 1984). Oxygen diffuses to the submerged roots through connected air-filled space in woody and non-woody stem and root tissues. In response to anoxic soil conditions, gas-conducting intercellular spaces arise through lysigenous and/or schizogenous processes, particularly in cortical tissues and sometimes in the stele of non-woody roots (lodgepole pine, Pinus contorta [Douglas ex Louden], Coutts and Phillpson, 1978). Intercellular space in secondary phloem and xylem accommodates oxygen diffusion from the stems to roots of some woody seedlings (Hook et al., 1971; Hook and Brown, 1972). In larger tree root systems, gas-filled vessels or tracheids may provide continuous, low-resistance pathways for longitudinal oxygen diffusion (Coutts and Armstrong, 1976; Phillpson and Coutts, 1980).

The present study investigates a hypothesis that continuous gas space in slash pine root wood allows long-distance transport of oxygen to submerged roots, conferring an ability to function during extended periods of anoxic soil conditions.

## Methods and Materials

The central root system of slash pine usually consists of a massive taproot that may divide at depth, plus several vertical branches or sinkers that arise at various points along the taproot and also from major laterals near their juncture with the taproot. Straight sections of such sinkers and of a small taproot were collected in April from two natural 24-yr slash pine growing on a wet flatwoods site, and from an 11-yr plantation-grown pine on a moderately well-drained site in the Austin Cary Forest near Gainesville, Florida.

The wet soil, an intergrade with Surrency sand (Arenic Umbric Paleaquult), was at the margin of a cypress pond where water stands above the soil surface for several months almost every year. At about 75 cm depth (the upper boundary of a gleyed sandy clay loam horizon, Btg, varied from 65 to 85 cm below soil surface), the pine taproots divided into several large tapering sinkers that terminated at about 150 cm depth. The distal portions of sinkers branched abundantly. Sections of sinkers were collected from between 25 and 150 cm.

The moderately well-drained Sparr sand (a Grossarenic Paleudult) consisted of 150 cm sand over a dense white sandy clay loam that stopped taproot penetration at about 170 cm. At 60 cm below the surface the taproot diameter was 10.5 cm. Sections were collected from this point downward and also from a smaller-diameter sinker root.

During an exceptionally dry period, a lateral root (6 cm diam.) of pond cypress (Taxodium ascendens Brongn.) was obtained 45 cm below the surface of a normally flooded soil. Smaller-diameter sinker roots were also collected from cypress laterals below the bottom of a lake margin.

Air content was immediately determined, as described below, for basal sections (about 12 cm diam.) taken from two wet-site pine sinkers, and for cypress sinkers. Additional sections of 12 sinkers (from two wet-site pines), the taproot and small sinker from the 11-yr plantation-grown pine, and the cypress lateral were trimmed of branches and stored in moist wrappings at about 4 C until used in air-flow and subsequent air-content determinations.

Air Content

Root sections from 2 to 12 cm diameter were stripped to the cambial surface, weighed, soaked briefly, and then submerged in water to determine green root volume by displacement. The sections were then dried at 100 C. Volume of cell wall (wood) substance was calculated by assuming a dry wood substance density of 1500 kg $m^{-3}$ (Panshin and de Zeeuw, 1970). Subtracting volumes of wood

substance and water from the total green volume gave the air-filled volume.

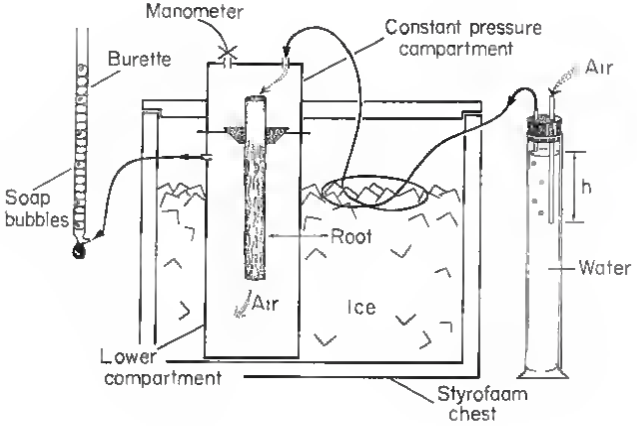
Ten samples dried initially to 65 C lost an additional 1.0 to 3.6% weight when subsequently dried to 100 C. Part of the additional loss presumably was due to volatiles other than water. Oleoresin contents probably would have been lower than the 4% (ww) extractive content of antire slash pine taproots, including stumps (Howard, 1973). Less than a quarter of this content is volatile at 100 C, however. Hence, the maximum overestimate of water content would have been less than 1%.

Air Flow

A preliminary experiment demonstrated that only 0.98 kPa of air pressure (10 cm water head) applied to one end moved a small unquantified amount of air through a 30 cm length of root. Subsequent falling-head experiments, with initial pressures of 1.18 kPa applied to a chamber enclosing one end of a root, showed a curvilinear decrease of chamber pressure with time, indicating a convective or Darcy-like air conduction through the root. The present study measured steady-state air flow when constant pressures between 0.06 and 0.98 kPa (0.6 to 10 cm water head) were applied to the confined basal ends of prepared root sections.

The steady-state air-flow procedure entailed sealing a root section into a two-chambered cylindrical apparatus (Figure 2-1). Constant air pressures were applied to the upper compartment in which the basal end of a root (about

Figure 2-1. Apparatus used for measurement of air flow through root sections.


Manometer
Constant pressure compartment
Burette
Air
Soap bubbles
h
Root
Water
Air
Ice
Lower compartment
Styrofoam chest

4 cm length) was confined. The remaining root length extended into the lower compartment, which remained open to the atmosphere through a modified burette. Air flow through the root was measured by the ascent rate of soap-film bubbles in the burette. The cylinder was housed in a styrofoam chest, and the lower chamber was surrounded by ice, maintaining a chamber temperature between 1 and 5 C to prevent resin exudation from the cut ends. Air passing through the roots had been water saturated and cooled.

Root sections were prepared from 10 wet-site sinkers, designated A to J for identification, the taproot and a sinker of the 11-yr pine, and a cypress lateral. The entire lengths of root A (approx. 50 cm) and the taproot (approx. 70 cm) could not be accommodated by the air-flow apparatus (maximum section length 40 cm), so these were initially divided into three, approximately equal-length sections. Additional sinker sections were not subdivided for initial air-flow experiments. Immediately before an experiment, however, at least a 2 cm length was cut from the ends of a root section, removing exposed xylem, major branches or distortions. The sawn ends were then smoothed with a chisel and new razor blades, removing 3 to 4 mm more from each end. Thus, most xylem elements were cut cleanly. The prepared ends were protected from subsequent wetting, drying or contamination. Preliminary experiments showed that air conduction through bark was negligible; hence, bark was removed from the basal 4 cm of each root section to

facilitate sealing into a conical plastic mold using warm 1:1 paraffin-petrolatum mixture. This seal separated the upper, pressure compartment from the lower, outflow compartment (Figure 2-1). The remaining bark surface was also coated with the mixture to prevent radial air escape from lenticels or surfaces of severed rootlets.

For each root section, air flow was measured at four or more successively greater pressures, increasing by increments of about 0.1 kPa, with at least three consecutive air-flow measures (rate of soap-bubble ascent) per pressure. Steady-state was assumed if the c.v. for air flow at a given pressure was less than 3%; the c.v. was usually less than 2%. The pressure sequences commonly ranged from 0.06 to 0.49 kPa, or, for long or more slowly conducting sections, from 0.49 to 0.98 kPa. Reproducibility of pressure-flow results was tested on two sections (the basal portion of root A, designated $A_b$, and root B) by repeating the same pressure sequences several times.

Following experiments with each section, the xylem cross-sections at distal and basal ends were traced onto a uniform paper. The tracings were cut out and weighed to determine areas; these ranged from 6 to 70 $cm^2$. Mean section length was obtained by several measurements around the circumference.

Most sinker roots tapered, so that the xylem cross-sectional area decreased toward the distal end. Thus, the length of a root influenced air flow by affecting pressure

gradient (kPa $cm^{-1}$) and the cross-sectional area. Shortening experiments with sinkers C to I entailed measuring air flow-pressure gradient relationships (as shown in Figure 2-3), first for the maximum root length, and then again after successive removal of one to three distal portions of each root. Distal (outflow) cross-section ($A_O$) increased with each shortening, of course, whereas areas of the basal (inflow) ends were not changed appreciably by reshaving before each run

Air Permeability

Steady-state flow of a compressible fluid through dried wood generally obeys Darcy's Law (Slau, 1971), stated as

$$Q/A = -K\Delta P/L \qquad (1)$$

where Q ($cm^3$ $min^{-1}$) is average flow rate through the entire cross-section A ($cm^2$), $\Delta P/L$ (kPa $cm^{-1}$) is the pressure gradient, and K ($cm^2$ $kPa^{-1}$ $min^{-1}$) is fluid permeability, a property of the conducting medium. Air flow-pressure gradient data for each root section were used to calculate air-permeability values according to Darcy's Law. Because the root sections had various dimensions, geometries and growth histories, they did not meet the basic Darcy assumption of an isotropic and uniform conducting medium. Thus, each permeability value was a unique property of its respective root section, not simply of the wood medium

## Results

### Air Content of Pine Root Wood

In this sample population some 48 to 69% of green root volume (inside bark) was air-filled (Figure 2-2a). Wood substance occupied 14 to 23% of the volume and water only 17 to 29%.

Absolute volumes of water ($V_W$) and wood substance ($V_X$) were very closely correlated ($r^2 = 0.998$) over a range of section volumes from 9 to 417 $cm^3$, despite variation in dry density from 180 to 350 kg $m^{-3}$. The regression is $V_W = 2.7 + 1.2\ V_X$. Transformation of the absolute values to percentages of green volume (Figure 2-2b), however, yielded a weaker correlation (Line A, $r^2 = 0.73$). Because percent wood substance and dry bulk density are interconvertible, Figure 2-2b reveals a trend of increasing total water content with root density. Reducing the total water content (Line A, Figure 2-2b) by an assumed fiber-saturation value of 30% we (Panshin and de Zeeuw, 1970) results in Line B, which indicates that the apparent lumen water content is also a function of root density. Increasing bulk density implies more cells with smaller lumina and/or thicker cell walls, but the relationship with lumen water volume is unknown.

Deep sinker-root sections, removed from >70 cm below soil surface (within the Btg horizon), were less dense (wood substance contents less than 17% vv), generally contained less water (11/13 sections less than 22% water vv), and thus

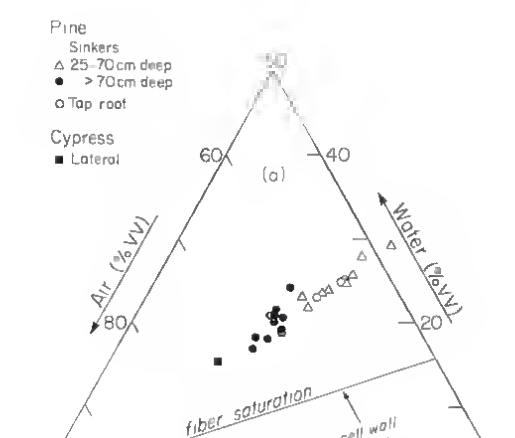



Figure 2-2. Air, water and wood substance volume in green root wood. (a) Proportion of air, water and wood substance volume in bark-free green roots of slash pine (and cypress). Fiber saturation as based on an assumed value of 30% (vv) of wood substance. (b) (next page) Percentage of total water (A) and lumen water (B) with percentage of wood substance (vv) root bulk density (wv). (see text) The difference between lines A and B is the fiber saturation value of 30%

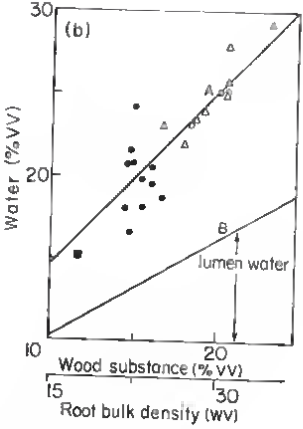



Figure 2-2--continued

had higher air-filled volumes than shallow sections removed from between 25 and 70 cm of the soil surface (Figure 2-2a). The shallower roots included basal sections of large-diameter sinkers and smaller diagonal branches of a massive taproot, suggesting that the cross-sectional area was not related to dry-root density. Sections of the taproot removed from below 70 cm depth in a moderately well-drained soil had similar wood properties to the shallower (less than 70 cm depth) wet-site pine sinkers.

Air Flow

Mass air conduction (k = AX, Equation 1) by individual root sections is defined here as air flow ($cm^3$ $min^{-1}$) per unit pressure gradient (kPa $cm^{-1}$) and has the reduced dimensions of $cm^4$ $kPa^{-1}$ $min^{-1}$ (i.e., does not consider root cross-sectional area). For root sections 8 to 40 cm long, mass air conduction was estimated from the slopes of linear air flow-pressure gradient relationships (Figure 2-3). All yielded $r^2$ greater than 0.98 for pressures ranging from 0.06 to 0.98 kPa.

Air conduction (slope of the air flow-pressure gradient relationship) increased by up to 18 and 14% between repeated air-flow experiments, respectively, roots A6 and B (Figure 2-3). It is likely that undetected effects of handling and repeated end surface preparation between experiments, e.g., smearing or wetting of a surface or,

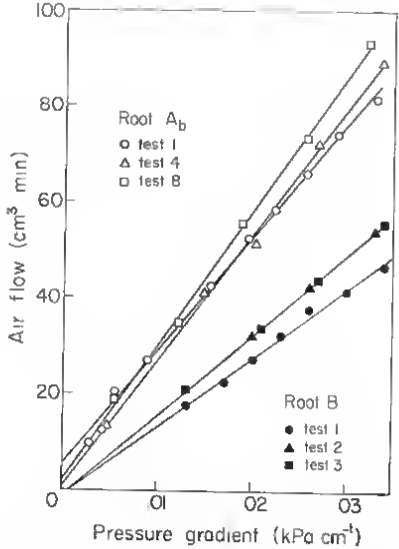



Figure 2-3. Linear relationships between air flow and pressure gradient in successive tests on two grass root sections of slash pine, Ab and B, respectively, 14.5 and 30 cm long. (Unreported tests 2, 3, 5, 6, 7 on root Ab involved partial coating of the outflow end surface with wax). Much of the difference between earlier and later tests is attributed to reshaving and surface contamination.

conversely, removal of plugged cells, produced some part of this variation (Choong et al., 1975)

Studies on a single root (Ab) demonstrated that coating portions of the air-outflow end with wax decreased air flow either in proportion to the area waxed or by a somewhat lesser amount. Coating the three, and then five, most recent growth rings reduced the unwaxed outflow-end surface by, respectively, 46.5 and 70%, and air conduction by 39 and 66%. When three quadrants or 75% of the distal end were waxed, air conduction decreased by 70%.

Air conduction increased as roots were shortened in five of seven sinkers tested (C to G, Table 2-1). The flow increased nearly proportionally with cross-sectional area of the distal (outflow) end ($A_O$) for roots E and F, but for others the air conduction increase was either less than (C and D) or greater than (G) the increase in $A_O$. Air conduction by additional roots, H and I (Table 2-1), did not increase with shortening, despite large increases in $A_O$. In fact, the decreases in air conduction for root I suggest handling error of the kind noted in the repeated tests above.

In general, mass air conduction increases linearly with outflow-end area ($A_O$, Figure 2-4) for the pine root population, including three taproot sections and a small sinker from the 11-yr pine and eight deep wet-site sinkers (removed from Btg horizon) with the shortened sections of sinkers C to I. $A_O$ explained 87% of the variation in air

Table 2-1. Effect of successive distal shortening of slash pine root sections (C to I) on increase in outflow area and air conduction.

| Root | Length | Basal area | Increase of distal end area[a] | Increase in air conduction[b] |
|---|---|---|---|---|
| | cm | $cm^2$ | % | % |
| C | 30.5 | 18.0 | 0 (10.8) | 0 (1080) |
| | 21.5 | | 37.0 | 17.9 |
| | 12.5 | | 50.9 | 23.8 |
| D | 32.0 | 11.1 | 0 (4.7) | 0 (667) |
| | 18.5 | | 29.8 | 16.0 |
| E | 24.0 | 44.4 | 0 (32.9) | 0 (2712) |
| | 14.0 | | 13.4 | 9.0 |
| F | 35.0 | 10.9 | 0 (6.2) | 0 (397) |
| | 18.0 | | 43.5 | 47.9 |
| G | 25.7 | 48.6 | 0 (23.3) | 0 (1491) |
| | 19.5 | | 14.2 | 33.8 |
| | 11.3 | | 52.8 | 74.3 |
| H | 23.0 | 7.0 | 0 (3.6) | 0 (662) |
| | 13.0 | | 52.8 | 0.9 |
| I | 39.5 | 19.2 | 0 (6.0) | 0 (1374) |
| | 28.0 | | 53.3 | -18.3 |
| | 20.5 | | 83.3 | - 5.5 |
| | 14.5 | | 111.3 | -14.2 |

a Values in parentheses are $cm^2$
b Values in parentheses are $cm^4\ kPa^{-1}\ min^{-1}$

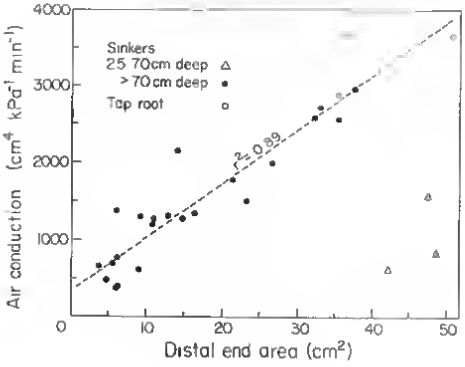



Figure 2-4. Relationship of mass air flow to distal end cross section. The correlation excludes values for three sections from less than 70 cm below the soil surface. Respective mean root lengths ± s.d. relative to air conduction: are 22±9, 21±8, and 16±5 cm, for less than 1000, 1000 to 2000 and greater than 2000 $cm^4$ $kPa^{-1}$ $min^{-1}$.

conduction for this population. The slope of this relationship, 68 ± $cm^2$ $kPs^{-1}$ $min^{-1}$, represents an average Darcy K value (Equation 1) describing the air permeability of green wood. The low permeabilities (i.e., low flow and yet relatively high $A_O$) of three shallow sections, B and J, removed from the basal ends of two main sinkers (less than 70 cm depth, Figure 2-4) were uncharacteristic of the main population. Two additional shallow branches from a wet-site taproot were also slowly air-permeable. They were not, however, included in Figure 2-4 because larger-diameter branches from each caused irregular cross-sectional area taper.

Comparison of Air Permeabilities

Air permeability ($K$) is the slope of the relationship between air flux ($Q/A$ $cm^3$ $cm^{-2}$ $min^{-1}$, Equation 1) and pressure gradient ($kPa$ $cm^{-1}$), having the reduced dimensions $cm^2$ $kPa^{-1}$ $min^{-1}$. The linear relationships for individual roots (Figure 2-3) and the general dependence of air flow on cross-sectional area (Figure 2-4) suggest application of Darcy's flow law (Equation 1) to compare air permeabilities among roots. Root taper, however, raises the question of which cross-sectional area is most appropriate: the larger inflow ($A_I$), the outflow ($A_O$), or some average. It happens that, for most roots, the cross-sectional area ($A(x)$ $cm^2$) decreases linearly with distance ($x$ cm) from the basal (inflow) end ($A_I$):

$$A(x) = A_I + bx \qquad (2)$$

Table 2-2. The root taper (b) obtained by least squares fit of n cross-sectional area measurements to Equation 2, for sinker roots and taproot with inflow (basal) cross-sectional areas, $A_I$

| | n | $A_I$ | b | $r^2$ |
|---|---|---|---|---|
| | | $cm^2$ | $cm^2/cm$ | |
| sinkers | 1 | 5 | 19.2 | -.3 | 0.98 |
| | A | 4 | 38.7 | -.7 | 0.95 |
| | G | 4 | 46.0 | -.9 | 0.99 |
| | C | 4 | 18.0 | -.2 | 0.91 |
| | B | 4 | 50.6 | -.7 | 0.72 |
| | F | 3 | 10.9 | -.1 | 0.93 |
| | E | 3 | 44.4 | -.5 | 1.00 |
| | H | 3 | 7.0 | -.2 | 0.98 |
| | D | 3 | 11.1 | -.2 | 0.96 |
| 11-yr taproot | | 3 | 69.7 | -.6 | 0.97 |

where b $cm^2$ $cm^{-1}$ is the rate of area taper, as shown in Table 2-2. If the length-area function, A(x), from Equation 2 is substituted for A in Darcy's equation, then

$$\int_{P_I}^{P_O} dP = -Q_{(X=L)}/K \int_0^L dx/A(x) \qquad (3)$$

where $P_I$ and $P_O$ (kPa) are, respectively, air pressures at the inflow and outflow ends, $Q_{(X=L)}$ is outflow measured at x = L, and L (cm) is the root-section length. Solving Equation 3,

$$Q\ (\ln A_O/A_I)\ (A_O - A_I)^{-1} = K\ (P_O - P_I)\ L^{-1} \qquad (4)$$

in which $A_I$ is the inflow-end area at x = 0, $A_O$ is the outflow-end area at x = L, and $(A_O-A_I)\ (\ln A_O/A_I)^{-1}$ is effectively an average cross-sectional area ($A_{AV}$). K (without subscript) then refers to air permeability for this average cross-sectional area.

K values for pine roots varied from 14.7 to 125 $cm^2$ $kPa^{-1}$ $min^{-1}$, with 21 of the 28 values falling within one standard deviation of the mean (Figure 2-5). $A_O$, obtained from Darcy's Law (Equation 1) using outflow area ($A_O$) rather than the larger average cross-sectional area ($A_{AV}$), is necessarily larger than K and so falls above a 1:1 line. For about one-third of the sinkers, $A_O$ is smaller than 80% of $A_{AV}$, and these high flow high taper root sections contribute most to the wide deviation of $K_O$ from K in Figure 2-5

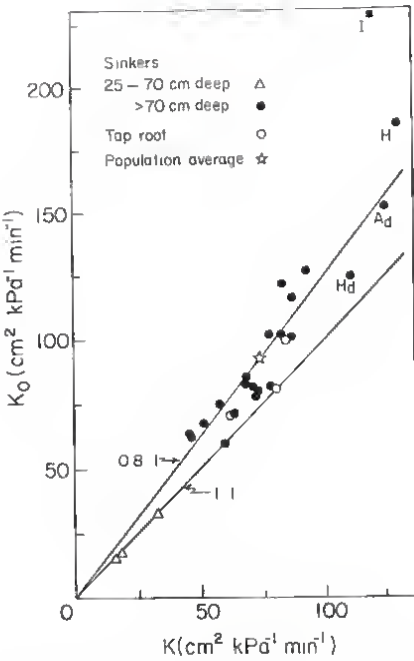



Figure 2-5. Air permeability (Darcy's K) of green slash pine roots based on distal (outflow) cross-sectional area ($K_0$) relative to that based on the average cross-sectional area as calculated by Equation 4 (K).

K values of some sections are unusually high, i.e., greater than 100 $cm^2\ kPa^{-1}\ min^{-1}$. They include roots H and I and the distal portions of roots A and H, designated as Ad and Hd, respectively (Figure 2-5). For roots H and I, air conduction is not apparently related to cross-sectional area (Table 2-1), suggesting that a single or few passages through the root conduct air, or that air permeability of the root increases distally sufficiently to compensate for the decreasing cross-sectional area.

Sections Ad and I, characterized by the highest K values (Figure 2-5), are also the deepest root sections studied. They had grown below 125 cm depth, where soil is continuously saturated. In contrast, the three least-permeable root sections were from the basal ends of two wet-site sinkers and had grown in a seasonally saturated environment. All of the other roots in Figure 2-5 were from below 70 cm depth and, with possible exception of the 11-yr pine taproot and sinker (grown in a moderately well-drained soil), had experienced frequent long periods of soil saturation.

Air Space and Air Permeability

Air permeability, K, is not clearly related to the proportion of air-filled volume in pine xylem (Figure 2-6). Although the least permeable basal sections contain the smallest air-filled volume of all pine sinkers studied, the most permeable sections are not those with the greatest air content. The remaining sinkers cover almost the entire

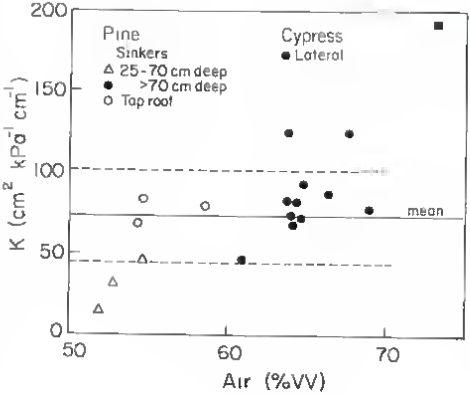



Figure 2-6. Scatter diagram of air permeability versus air-filled volume. The dashed lines indicate ± 1 standard deviation from the mean permeability.

ranga of air volume encountered in pine up to 0.69 $cm^3$ $cm^{-3}$. By way of contrast, a large cypress lateral (26 $cm^2$ av. cross-section) had an air content of 73% and greater longitudinal air permeability, 192 $cm^2$ $kPa^{-1}$ $min^{-1}$. The high air permeability and low dry bulk density are consistant with values for a few other cypress sinkers examined.

## Discussion

The average proportion of air-filled space in green slash pine stemwood ranges from 15 to 22% (calculated from data given by Schroeder and Phillips, 1972; Howard, 1973). In contrast, air content in the green rootwood of the present study ranged from 49 to 69%. This is far higher than in other pines or, indeed, in conifers other than Taxodium that have been examined. Lateral roots of lodgepole pine, for example, contained 19.3% air space, including longitudinally continuous bands of embolised latewood tracheids, whereas Sitka spruce (Picea sitchensis [Bong.] Carr) had only 5.6% (Philipson and Coutts, 1980).

The high air content is a consequence of both low bulk density and low water-filled volume. Densities of slash pine tap and sinker roots (260 kg $m^{-3}$, s.d. 40) are much lower than those of southern pine stemwoods (470 to 560 kg $m^{-3}$, from Schroeder and Phillips, 1972; Howard, 1973) but encompass the same range given for vertical and lateral roots of red pine (Pinus resinosa Ait., Fayle, 1968).

Denaltiaa of vertical alash pine and red pine roots tend to decreaee dietaliy. Thia ie in accord with other reports that wood calls tend to be iongar, wider and thinnar-walled with increaaing diatance from the bole (Bannan, 1941; Manwiller, 1972). The avarage green moisture content of alash pine roots (87% oven-dry weight, s.d. 8) ie in the middle of a broad range given for pine woods (36% to 124%, from Choong, 1969; Schroeder and Phillips, 1972; Howard, 1973; Mardan et al., 1975) but, with the iow bulk denaity, only 17 to 29% of root voiume ia water-filled.

Intercellular apacea are uncommon in normal aecondary xylem of the Pinaceae and apparently are not continuous (Bolton et al., 1975). Calculations for the ainker aection $A_b$, having 14.7% wood aubatance, 20.8% water and 64.3% air by volume, ahow that air ia moatly in the cell iumina; thua, if molat call walls have an air-filled porosity equal to either a) the water-filled porosity (i.e., water volume at fiber aaturation moisture content, 30% o d.w.) or b) one-third of that, then the total lumen (cell lumina) volume would be only a) 19.7% or b) 18.6% water-filled, with the remainder occupied by air. Almost certainly, for normal xylem conduction to occur, most of the free water must be within a limited number of connecting water-filled tracheids. Likewise, entirely air-filled tracheids, with or without partiaipation of ray tiaaue (Back, 1969), would provide a network through which either mass flow or diffuaion could occur.

Roots offer little resistance to longitudinal mass air movement, and flow results from pressure gradients as small as 0.002 kPa $cm^{-1}$ (0.02 cm water $cm^{-1}$) (Figure 2-3). In accordance with Darcy's Law (Equation 1), air flow increases with pressure gradient, not as the result of new flow passages being opened, and without apparent gas compression (Taylor and Ashcroft, 1972; Laub and Pecsok, 1978). The applied pressures, from 0.06 to 0.98 kPa, are only great enough to drain water-filled capillaries of 4.9 to 0.3 mm diameter, respectively (calculated from $P = 4\gamma/d$, where pressure, P, is proportional to the surface tension of water, $\gamma$ = 73 dyn $cm^{-1}$, and the inverse diameter, d (Hillel, 1980)). In order to conduct air, therefore, tracheid lumina that vary from 0.036 to 0.046 mm diameter in southern pine root wood (Manwiler, 1972) must be already air-filled.

As would be expected, air conduction is linearly related to cross-sectional area for the sample population as a whole (Figure 2-4), except in shallow sinker sections. The slope 68.6 $cm^2$ $kPa^{-1}$ $min^{-1}$ represents an average air permeability regardless of root dimensions. The permeabilities, K and $K_Q$, for individual roots (Figure 2-5) incorporate unique effects of geometry and xylem deformity (Table 2-1), although some effect of root taper is removed from K in calculating the average cross-sectional area (Equation 4).

Air permeabilities, K, are mostly between 50 and 90 $cm^2$ $kPa^{-1}$ $min^{-1}$ (Figure 2-5). This is small, given the large

volume of air-filled space in roots. For example, pine sinkers C and E, with air-filled porosities of 69 and 65%, and average diameters of 4.2 and 7.0 cm, respectively (Table 2-1), are as resistant (1/K) to air flow as capillaries only 0.6 and 0.8 mm diameter. The latter would represent only about 0.02% of the root cross-sectional areas (calculated by equating Darcy's Law and Poiseuille's Law for viscous flow, $Q = (\pi r^4/\mu)P/L$, where r is the capillary radius and air viscosity $\mu$ = 170.8 $10^{-6}$ poise). Darcy K estimates suggest that the green wood of slash pine tap and sinker roots is about as conductive to air as dry pine sapwood, e.g., 59 $cm^2$ $kPa^{-1}$ $min^{-1}$ (Siau, 1971) and 70 $cm^2$ $kPa^{-1}$ $min^{-1}$ for air-dried southern pine sapwood (Choong and Fogg, 1968). Thus, high resistance in green root wood is consistent with the conduction being primarily through interconnected axial tracheids, as it is in dried pine wood (Siau, 1971).

Generally, air permeability proved independent of length up to at least 40 cm (Figure 2-4), indicating a continuity of air-filled pores that favors long-distance gas exchange through sinker wood. Although the bordered pit structure in tracheids should prevent formation of continuous air emboliems, more so in earlywood than latewood (Bailey, 1957; Gregory and Petty, 1973; Esau, 1977; Bolton and Petty, 1977), emboliem in the latewood of pines and certain other conifers may provide permanent longitudinal and tangential pathways for gas diffusion or mass flow (Coutts and Armstrong, 1976). In large lodgepole pine

laterals, air bubbles emerged from the cut ends of embolised latewood up to at least 50 cm from the air-inflow end (Philipson and Coutts, 1980). With air conduction by green slash pine roots being strongly related to the cross-sectional area, however, it is unlikely that the interconnected air space is confined to latewood. The relatively narrow bands, presumed latewood, were only a small proportion of the total root xylem, suggesting that the earlywood is also extensively embolized and air-conducting.

The pathway through which mass air-flow occurs is equally available for gaseous diffusion, the most probable mechanism for replacing oxygen consumed by respiration of roots below the water table (Armstrong, 1968; Armstrong and Read, 1972). Diffusion depends primarily on total volume and tortuosity of continuous pores rather than upon pore-size distribution, as mass flow does (Hillel, 1980). Darcy K was not related to the air-filled porosity of root xylem (Figure 2-6). The high proportion of air-filled space in green sinker wood, however, is particularly suited for oxygen diffusion, with the large air-filled volume serving as a pool facilitating exchange between the atmosphere and respiring tissues.

Thus, the xylem of the central root system of this species appears to have a dual role in transport, conducting water and solutes through a portion of its cross-section (up to 20 to 30%) while allowing gas flow or diffusion through

some largs part of the rsmaindsr. This occurs dsspitm the inhsrent limitations of coniferous xylsm. Furthermore, msintsinsnce of s large proportion of sir-fillsd spscs in roots thst may be 1 to 2 m below ths water tabls obviously implies s cspscity to sxclude wstsr undsr positive prssours, ss well ss to sbsorb it.

Root System Ventilation

Another study dsmonstrstes thst potassium uptsks by or sfflux from submerged slash pins roots occurs when the sttsched stem snd bssal roots srs sxpossd to sn sir or nitrogsn stmosphsrs, respectivsly (Chapter 4). Thess results, plus litersture rsfsrencss snd our obsservstions, lssd to s cohsrent visw of how ths submerged roots of slash pins srs ventilstsd.

Littls is known of gss sxchsngs rstss betwssm ths stem or bssal root sections snd ths stmosphsre. In many flood-tolsrent woody species, howevsr, hypertrophisd lsnticsls, whlch prolifsrste in snd just sbove ths normslly ssturstsd soil zons, srs ths primary points for $O_2$ sxchsngs (Armstrong, 1968; Hook st sl., 1970 snd 1971; Coutts snd Philipson, 1978; Coutts, 1982; Topa snd McLeod, 1986b). In lsrge lstersls of lodgspole pins (Philipson snd Coutts, 1980) snd ths seedling stems snd roots of some wetlsnd snglosperms (Hook snd Brown, 1972), $O_2$ diffusss rspidly through ths interconnsctsd intercellular spscss of lsnticsls, phlosm rsys snd cambium, into ths xylsm rsys snd sxisl xylsm slsments. A similsr gss-diffusion psthway must

occur in slash pine, i.e., from the atmosphere to the longitudinally conductive air-filled tracheids in root wood and, ultimately, into root-tip lacunae as discussed later.

Elongate lenticels, often hypertrophied, are common near the base of the taproot and sinkers and on adjacent shallow laterals. Exchange through stem lenticels alone must suffice for slash pine growing in shallow ponds where water stands above the soil surface continuously for several months or a few years at a time.

Wet-site conditions affect slash pine root system morphology by reducing the depth to which vertical roots grow; increasing branching; and generally causing higher cross-sectional area to length proportions. Produced in response to soil saturation and the constrained soil-$O_2$ supply, this gross morphology, in turn, seems adapted for efficient internal $O_2$ diffusion to submerged roots. The taproot (which is often a composite structure incorporating fused major and minor sinkers) is massive; its diameter 1 m below the soil surface may equal or exceed stem xylem diameter 1 m above. It is supplemented, and sometimes replaced, by a few to several large diameter sinkers (e.g., 3 to 15 cm diameter, 0.5 to 2 m long) that extend as much as 1 m below the mean water table (Schultz, 1972). The latter taper gradually. Where submerged, commonly three vertical rows of short branches descend from the sinkers and lower taproot. One to four higher orders of branching occur in often densely arranged fans or clusters, oriented by the

generally diarch structure of the parent root. Even the terminal rootlets are relatively thick, about 0.1 to 0.2 cm diameter (0.5 to 7 cm long), although continuous indentions by appressing sand grains often reduce the root cross-sectional areas. Dense branching provides a relatively large surface area of small-diameter, absorbing roots in the saturated zone, with a reduced $O_2$-diffusion path-length from the soil surface to distal ends. Large xylem cross-sections, particularly for the lower-order basal roots, apparently provide greater capacity for gaseous exchange.

It is not yet clear how the gas-filled space in root wood communicates with the primary xylem tissues of root tips. The distal portions of submerged rootlets, however, may contain--and probably generally do contain--longitudinally continuous gas-filled lacunae located within the pericycle and between the xylem poles of the primary stele. These are compressed by secondary thickening and eventually obliterated after a continuous cambium forms. For slash pine seedlings grown in saturated peat-sand medium, stelar lacunae occurred only within 5 cm of root apices, beyond which there was advanced secondary thickening. The frequency, length and duration of such aerenchyma have not been studied but appear generally similar to those reported from flooded seedlings of loblolly pine (Pinus taeda L., Topa and McLeod, 1986b; McKevlin et al., 1987) and lodgepole pine (Coutts and Philipson, 1978). In the latter, the presence of longitudinal lacunae was

clearly related to the rapid diffusion of $O_2$ from stems to primary-root tips.

The foregoing description applies only to the central root system. It seems likely that a similar opportunity for diffusion may be found in sinkers descending from large laterals on or in the soil surface, as sometimes seen in older trees on perennially wet soils. At times when such laterals are submerged by a high stand of the water table, however, the diffusion-path length alone probably would prevent a useful air supply from the central stem to distant sinkers.

Results in this paper refer to roots developed with some exposure to poor soil aeration. Slash pine roots grown on well-drained soils may not have the properties discussed, although we have no evidence to this effect except reports of fine-root damage in slash pine on sites with fluctuating water tables (White and Pritchett, 1970) and reduced nutrient uptake function when roots are suddenly subjected to low aeration (Shoulders and Ralston, 1975). Although woody roots of tolerant species have not yet been shown to increase secondary xylem porosity in response to waterlogging (Philipson and Coutts, 1980), the distal portions of slash pine sinkers, grown into perennially saturated anaerobic soil, have high air-filled porosities and the greatest air-permeability values. Non-woody roots of lodgepole pine (primary tissue structure) developed longitudinal lacunae and the capacity to oxidize their root

surfaces only when grown in anoxic conditions (Coutts and Phillpson, 1978; Phillpson and Coutts, 1978). Similarly, in loblolly pine the iron-oxidizing, $O_2$-conducting lacunate roots were not produced in well-drained aerobic soil (Hook and McKevlin, 1987; McKevlin et al., 1988). A similar conditioning will probably be found in slash pine.

CHAPTER 3
IRON OXIDE PRECIPITATION ON SLASH PINE ROOTS:
AMOUNTS AND IMPLICATIONS

## Introduction

Iron oxide deposits commonly occur on roots growing in reduced saturated soils (Armstrong, 1982). Such precipitates are most evident on herbaceous and shrubby species endemic to wetland habitats (Armstrong and Boatman, 1967; Armstrong, 1968) but are also formed on the roots of some mesophytes that tolerate temporarily saturated soil conditions (Bartlett, 1961). The capacity for Fe(II) oxidation is related to $O_2$ leakage out of roots and, accordingly, to internal $O_2$ transport to the submerged portions of root systems.

The soil processes that govern Fe oxide accumulation around oxidizing roots are analogous to those that govern Fe oxidation in the surface layers of submerged soils (Howeler and Bouldin, 1971).

There are relatively few reports of Fe oxides on tree roots. Swallow (1855) noted Fe-enriched zones around live and dead roots of white oak (*Quercus alba*). Dickson and Broyer (1972) observed that Fe deposits were present on roots in almost all cases where water tupelo (*Nyssa aquatica* L.) and bald cypress (*Taxodium distichum* L. Rich.) were

cultured in saturated soil, and that more reduced soil conditions lead to greater Fe(III) deposition. The oxidative capacity of tupelo roots was clearly related to adaptions that allowed $O_2$ transport to the submerged roots (swamp tupelo, Nyssa sylvatica var. biflora [Walt.] Sarg., Hook et al., 1970 and 1971; water tupelo, Hook and Brown, 1972). Flooded roots of mesophytic loblolly pine (Pinus taeda L.) seedlings accumulated Fe(III) within the epidermal and cortical tissues with some lighter deposits within the stele (McKevlin et al., 1987). Hook and McKevlin (1988) showed that $O_2$ diffused from the above-soil atmosphere into the stales of submerged loblolly pine roots but that radial $O_2$ losses were small. Deposits of Mn and Fe oxides were similarly located in the flooded-seedling roots of other conifers (black spruce, Picea mariana Mill., and red pine, Pinus resinosa Ait., Levan and Rhia, 1986).

The present study investigates the oxidizing capacity of slash pine (Pinus elliottii Engelm. var. elliottii) roots. The site tolerance of slash pine appears intermediate between hydrophytic species like cypress and tupelo that experience prolonged inundation of the entire root systems and mesophytes that can survive only relatively short periods of inundation except during seasonal dormancy. In poorly drained flatwoods of the lower coastal plain of southeastern United States, slash pine grows naturally on the margins of ponded depressions with pond cypress (Taxodium ascendens Brogn.) growing within. On such sites,

the surface root system of slash pine is periodically submerged, but the massive taproots and sinkers of slash pine grow to depths as much as 0.5 m below seasonally low water-table levels into continually saturated soil (Schultz, 1972). In Chapter 2, it was shown that the deep submerged roots were aerated by the exchange of $O_2$ between the atmosphere and the large volume of air-filled space in secondary xylem. For lodgepole pine (Pinus contorta Douglas ex Louden), Phillipson and Coutts (1978 and 1980) showed that $O_2$ movement through secondary xylem and lacunate stelae sustained a radial diffusion of $O_2$ from woody and non-woody roots, allowing oxidation of the rhizosphere. The studies reported here hypothesize that the rhizospheres of submerged slash pine roots are similarly oxidizing and so should accumulate Fe oxide on or within the roots. In one study, Fe(II) was introduced into the saturated low-Fe medium in which slash pine saplings were growing. In the other, the nature of Fe oxide deposits formed on roots of mature, field-grown slash pine root systems was examined.

## Methods and Materials

### Study 1: Saplings

In spring 1983, four 1-0 slash pine seedlings were planted in each of twenty 130 L steel drums, 85 cm high. The drums were steel-brushed and coated inside with an asphalt-based paint. Two 1 cm diameter drainage holes were drilled 15 cm below the upper rim on opposite sides. Drums

were filled to a depth of about 15 cm with sand (Quartzipsamment subsoil), and then with a local acid peat (medaprlat, pH 4.5 water, ash 14%, C/N 18.8, total Fe 0.95 g $kg^{-1}$, Munson, 1982) to within 5 cm of the upper rim. The seedlings were planted deeply, with root collars about 5 cm below the peat surface and taproots extending to as much as 25 cm. At 5 mo, the two smaller seedlings were removed from each drum; the third was removed at 11 mo, leaving one sapling/drum. Concentrated superphosphate (7 g P/drum) was mixed with the peat at planting, 20 to 25 cm below the surface, and macro-nutrients were added periodically thereafter.

Initially, the sand and peat were saturated by gradual water addition from above. For the next 12 mo, deionized water was added on alternate days until there was overflow from drainage holes. The holes were stoppered between watering, so rainfall additions occasionally ponded water over the peat surface.

At 12 mo, a 20 cm deep well was bored in the surface peat of each drum and fitted with an open pvc pipe (3.5 cm i.d.) with several 0.5 cm diameter holes drilled around the circumference. A 2.5 L Mariotte bottle supplied deionized water to the well in response to water use by the saplings. With the drainage holes stoppered, the Mariottes maintained water-table levels approximately 10 cm below the peat surface. The bottles generally held enough water to supply the 24 h water use by saplings.

Detecting redox conditions

Oxidizing conditions in the peat were indicated by patterns of rust formation on steel rods. Thin straight rods (survey-flag supports) about 70 cm long and 2 mm diameter were rubbed with steel wool to expose unoxidized metal, then inserted into peat to depths of about 65 cm. The rods were withdrawn after periods in peat of up to 6 months, and examined for rust formation.

One platinum (Pt)-tipped wire electrode was inserted into each of twelve peat-filled drums; six electrodes were between 25 and 30 cm deep and six between 40 and 45 cm. By using a portable voltmeter, the Pt-electrode measured the saturated-peat Eh (electrochemical potential) relative to a calomel reference electrode placed into the wet surface.

Iron(II) placement in saturated peat

After 18 months growth in peat, the saplings were 1.7 ± 0.5 m in height and used water at a maximum daily rate of 1.9 ± 0.3 L $d^{-1}$. At this time a 2% (wv) Fe(II) solution was introduced below the water table of all drums. $FeCl_2$ was dissolved in a reducing solution of 0.2% ascorbic acid and 0.1% glucose, adjusted to pH 3.6. About 50 $cm^3$ of this solution (approx. 1 g Fe) was added to each of two open-ended glass tubes (1 cm i.d.), inserted 20 and 40 cm vertically into the peat at radial distances of 10 cm from the sapling stem. After the solution had drained slowly to the water-table level, the tubes were stoppered and left in place.

Sampling roots and peat

One year after Fe(II) was introduced below water tables (8/85), the root systems of six saplings with generally larger crowns and greater water use were removed from peat and examined for accumulations of oxidized Fe. The sapling heights varied from 2.0 to 2.5 m, and stem diameters at 10 cm above the peat surface varied from 4.2 to 5.2 cm. On high water-use days these had drained all the water from 2.5 L Marlotte vessels. The stems were cut about 15 cm above the peat surface, and the lateral root systems were severed in a 20 cm radius from the stem to about 25 cm depth, with a long-bladed bread knife. The root mass was lifted from the drum, length to the deepest root tip measured, and peat adjacent to the root system was grab sampled. The deepest 10 to 15 cm of each root system was detached and immediately washed in 1 M ammonium acetate and then in deionized water to remove loose peat particles and soluble Fe(II). Wet peat and root samples were stored in polyethylene bags at 4 C.

Root and peat analyses

Washed roots were separated into diameter classes (<1 mm (very fine) and 1 to 3 mm (fine)], and root lengths were estimated by the line intersect method (Newman, 1966). Determinations of total Fe in roots and peat are described later under Study II.

The moisture content of wet peat was determined by oven drying at 65 C. For estimation of soluble and exchangeable-

Fe content, wet peat samples (50 g) were extracted (30 min vigorous shaking) in 50 $cm^3$ of 1 M ammonium acetate adjusted to pH 4 (Olson and Ellis, 1982). The pH of 1:1 wet peat:deionized water suspensions was measured with a glass combination electrode.

Fresh hand-cut sections of the distal root tips, and the oxidized ash remaining after several root tips were heated in a muffle furnace for 2 h at 550 C were examined under a light microscope.

Study II: Mature Trees

Unusually low water tables allowed excavation of the central taproot systems of two neighboring, 24-y slash pine in the Austin Cary Forest, near Gainesville, Florida. The trees, 20 cm inside-bark diameter (80 cm above ground), grew on the margin of a shallow depression that was ponded for several months in most years, and that supported growth of only a few pond cypress trees.

Hydromorphic processes dominated soil development across the depression (Figure 3-1). In the middle, the pedon was a Surrency sand, an Arenic Umbric Paleaquult, having a thick mucky sand surface (A1) to 45 cm depth and dark-gray sand (Bh, 45-95 cm) over a gray-brown sandy-clay loam (Btg1) and sandy clay (Btg2). Soil at the margin of the pond had less organic matter in the sandy horizons above the Btg (Table 3-1), reflecting the shorter duration of surface saturation. Across the depression, the Bt was gleyed (chromas $\leq 2$) with dark-brown to red streaks (chromas

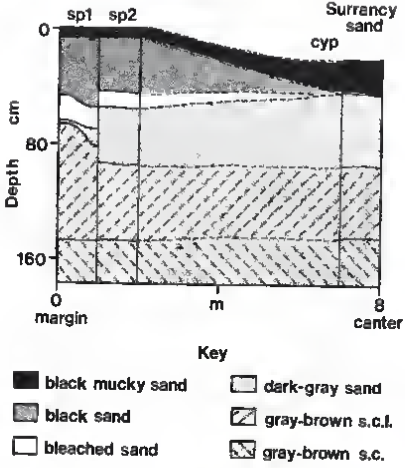



Figure 3-1. Horizon development across the dry pond, interpolated between descriptions of the pond margin pedon obtained from root system excavations of two slash pines (sp1 and sp2), and in the mid-pond pedon with cypress (cyp)

Table 3-1 A profile description of soil surrounding an extracted slash pine root system on the margin of a shallow landscape depression, and gradational to the mid-depression Surrency Sand.

| Horizon | Depth | Texture | Matrix Color | Mottles Color | Mottles Description |
|---|---|---|---|---|---|
| O | +5-0 | coarse pine litter | | | |
| A1 | 0-5 | s | 2.5Y 2/0 | none | |
| A2 | 5-55 | s | 2.5Y 2/0 | none | |
| E | 55-67 | s | 2.5Y 5/2 | 2.5YR 4/4 | common; tubules |
| Bh | 67-84 | s | 2.5Y 4/2<br>2.5Y 6/4 | 2.5YR 4/6 | and nodules with fine root or pore st center. |
| Btg1 | 84-135 | scl | 2.5Y 5/2 | 7.5YR 4/6<br>5YR 4/6 | common; surrounding fine root-like pores, weakly or strongly cemented. |
| Btg2 | 135-165 | sc | 2.5Y 5/2<br>5Y 5/2<br>5Y 6/1 | 7 5YR 4/6<br>5Y 4/6 | few; as in Btg1 surrounding root-like pores |

≥ 3) along root channels (fine to coarse). Prominent yellowish-red mottles, all neoferrans (Brewer, 1964), surrounded fine root-like pores in the E and Btg horizons.

The central root systems of each sixth pine consisted of a massive taproot from which the surface laterals branched. This taproot divided at about 55 cm into several straight-sided sinkers that extended into the Btg. Sinkers tapered to blunt points or several fingering branches as much as 150 cm below the soil surface. Three or four vertical flies of 1-order adventitious roots (2 to 3 mm diam.) branched from the distal 20 to 30 cm. Otherwise, the sinkers had only a few coarse branches.

Sampling roots and soil materials

Sinker roots were collected for another study (Chapter 2). Before storing the roots in moist wrappings at 4 C, weakly adhering high-chroma materials were scraped from their surfaces and air-dried. High-chroma rinds of strongly cemented sand were not removed from roots until after sinkers had been stripped to the cambium for other measurements. Then, the air-dried rinds were scraped from root surfaces and hand-ground to pass a 1 mm mesh. Soils were described from within the two pits and from auger holes at the pit margins. Munsell colors of wet matrix materials and neoferrans were determined. High-chroma materials, ≥ 4, and the low-chroma soil matrix, ≤2, in each of the E and Btg horizons were separated and sampled. Loose sandy materials in the E horizon were excavated directly from within the

pits and stored field-moist at 4 C. Clods from the argillic horizon (64 to 134 cm depth) were collected and stored in a moist condition at 4 C. Subsequently, the high-chroma mottles and low-chroma matrix materials were picked out. Fine to medium roots encased in high-chroma soil materials were also collected from the clods and air-dried.

At the middle of the pond, soil and root materials were collected from the sandy-clay subsoil between depths of 135 and 170 cm (1.4 m from the nearest cypress and 6.2 m from the nearest pine on the pond margin). Soil and root materials were also sampled from about 60 cm depth at the base of a mature cypress tree in a neighboring pond.

Freshly exposed soil surfaces were treated with ortho-phenanthroline solution to reveal the distributions of Fe(II), which could be compared with proximity of Fe(III) in neoferrans and root coatings.

Ash extraction of root material

Dried roots ≤2 mm diameter with attached high-chroma soil materials, and rinds of skinkare were ashed at 550 C for 3 h. The cooled ash was treated with 10 $cm^3$ of 40% HCl, heated to dryness, treated again with 5 $cm^3$ of concentrated HCl, and again dried. The salts were then dissolved in 10 $cm^3$ of 0.1 M HCl and quantitatively transferred to either 25 or 100 $cm^3$ volumetric flasks, depending on sample size. Dissolved Fe was determined colorimetrically by the o-phenanthroline method (Olson, 1965).

Soil extractions

Dithionite-citrate-bicarbonate. Field-moist samples of the soil matrix and neoferrans (equivalent to 10 g o.d.w.) were extracted twice by shaking with dithionite-citrate-bicarbonate solution for 16 h periods, without heat treatment (Kunze, 1965). Clear extracts for each sample were combined and made to one-litre volume. Aliquots of the combined extracts were treated with $H_2O_2$ to remove excess dithionite, acidified, and transferred to 50 $cm^3$ volumetric flasks. Iron was determined by atomic absorption spectroscopy. Smaller amounts of air-dried rind materials were treated similarly.

Acidified ammonium oxalate. Field-moist samples (equivalent to 1 g o.d.w.) were shaken in 100 $cm^3$ of acid-oxalate reagent (McKeague and Day, 1966) in a 250 $cm^3$ centrifuge bottle on a reciprocal shaker for 4 h. Suspensions were then immediately flocculated, centrifuged and filtered. Aliquots of 25 $cm^3$ were diluted to 50 $cm^3$ with acidified-CsCl solution and analyzed for Fe by atomic absorption spectroscopy (Searle and Daley, 1977).

Total phosphorus. One-gram samples of oven-dried soil or rind, passed through 1 mm mesh, were ashed at 520 C for 4 h. The cooled ash was treated with 10 $cm^{-3}$ concentrated HCl and boiled for 4 h at 125 C. The samples were then diluted to 50 $cm^{-3}$, allowed to settle, and P determined by the Murphy and Riley (1962) procedure.

## Results

### Study I: Saplings

#### Root depth and redox conditions in peat

Roots of the six saplings extracted during the fourth growing season extended to depths of 33 to 55 cm (44.7 ± 8.0 cm) below the peat surface. During high water-use summer months, water tables fluctuated in short cycles between a high level at 10 cm depth and several centimeters below that, because water use by saplings often drained Mariotte vessels between alternate days' refilling. The oxidizing peat surface, Zone I, indicated by orange rust-formation on steel rods, extended to a depth of 16 ± 6 cm (3/84 - 8/84, Table 3-2). During rainy periods, water tables remained near or above the 10 cm depth, and the depth of rusting was limited to about 4 cm below surface, (8/85, Table 3-2).

Below the oxidized surface, in Zone II, the surfaces of rods were pitted and partially coated by a thin black scale (possibly a Fe(II)/Fe(III) hydroxy compound, Schwertmann and Taylor (1977)). The affected surface area decreased from >50% near Zone I to a negligible proportion at the lower boundary (30 cm, 3/84-8/84, Table 3-2). Below Zone II, rods were not pitted or scaly. A color change from dark gray to orange following exposure to air indicated the presence of Fe(II) on the unencrusted parts of rods.

One month after withdrawal of the iron rods (9/84), the average redox potential in the peat at depths of 25 and

Table 3-2 Mean depth extent of Zone I from the peat surface and the average maximum depth of Zone II. Study I.

| Period in Peat | Rods/ Drum | Depth Extent Zone I[a] | Zone II[b] |
|---|---|---|---|
| | | cm | |
| Pre-Mariotte | | | |
| 7/83-2/84 | 4 | 14(5) | 44(14)[c] |
| With Mariottes | | | |
| 3/84-8/84 | 5 | 16(8) | 30(16)[d] |
| 8/85 (wet) | 2 | 4(1) | 16(4) [e] |

a Zone I, orange rust formed on steel rod
b Zone II, pitting and black scale on steel rod.
c Mean (s.d.), 2 rods removed 9/83 and 2 rods removed 2/84 for each of six drums
d Rods removed after 4 and 6 months in peat.
e Rods in only 4 drums.

45 cm was -21 ± 74 mV (relative to S.H.E.). This means represented an average condition for Zone II (non-rust-forming corrosion) and the non-corrosive zone below that. The pH of peat:water (1:1) slurries varied from 4.0 to 4.5.

Iron precipitation on and within deep roots

Sapling taproots were about 10 mm in diameter at 10 to 15 cm behind the distal tips, and tapered to thick apices 2 to 3 mm in diameter (Figure 3-2). As many as two orders of short fine rootlets divided from woody 1-order branches of each taproot. After washing and air-drying, root coloration varied from strong brown to black. An amorphous brown material bound peat fibers and white-hyphal structures to the external root tissues. The apices of lower-order roots, in particular, were thickly encrusted, black and misshapen. Behind the apices for some 2 to 5 cm, the dead peripheral tissue consisted of dark-colored elongate cells that concealed fine aggregated precipitates, pale yellow to yellowish-red, either coating or filling the subsurface cells. The oxidized ash of various root type <3 mm diameter consisted of 1) dark-red cell casts (notably smooth and shiny on one side) and fine porous coatings of yellowish to dark-red oxides, which together defined the encrusted external tissues, 2) white ash replacing the xylem core. Iron comprised some 24 to 154 g $kg^{-1}$ of such roots (Table 3-3). The greatest Fe accumulations occurred in the black-encrusted 1-order root apices of sapling 2, and on the fine roots of sapling 3, all of which were thickly coated with a

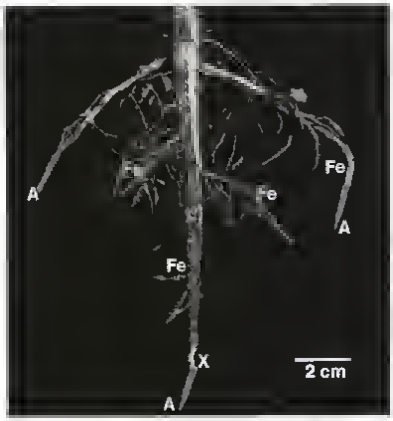



Figure 3-2. Distal 13 cm of the taproot of sapling 3, showing heavy iron oxide precipitation on distal ends of 0- and 1-order roots and on all higher-order roots. Study I. Taproot tip is 49 cm below the peat surface. A, iron oxide-encrusted root apex; Fe, iron oxide-cemented peat; X, exposed secondary xylem core without iron oxide. (See Table 3-2)

Table 3-3 Iron precipitation on end in 1- to 3-order very-fine end fine roots sampled from the distal ends of taproots, together with total and exchangeable iron in the surrounding peat. Study I

| Sapling | Roots | | Peat[a] | |
|---|---|---|---|---|
| | <1mm | 1-3mm | Total | Exchangeable |
| | | | Fe, g $kg^{-1}$ dry wt. | |
| 1 | - | 30 | 2.6(.5) | 0.14(.01) |
| 2 | 100 | 154 | 3.2(.8) | 0.58(.40) |
| | 95 | 140 | - | - |
| 3 | 123 | - | 1.3(.1) | 0.20(.15) |
| | 112 | - | - | - |
| 4 | 50 | 59 | 2.5(1.0) | 0.34(.03) |
| | 70 | 60 | - | - |
| 5 | 54 | - | 3.5(.9) | 0.56(.18) |
| 6 | 50 | 51 | 3.9(1.4) | 0.55(.60) |
| | - | 24 | - | - |

a Mean (s.d.) of two or three samples from 20-50 cm depth.

strong-brown precipitate (Figure 3-2). Iron contents of those roots were from 30 to 95 times the total Fe content in surrounding peat (Table 3-3). Roots with less apparent surficial-oxide deposits (saplings 1, 4, 5 and 6) had also accumulated Fe to concentrations much greater than those in the surrounding peat.

Estimated lengths and diameters for roots of sapling 4 (Table 3-3) allowed conversion of the total Fe contents to terms of root surface area. For the very fine roots <1 mm diameter, the areal Fe contents became 0.3 and 0.4 mg $cm^{-2}$, in contrast to 0.9 and 0.6 mg Fe $cm^{-2}$ for apices of 0- and 1-order roots from 1 to 3 mm diameter. These values are not strictly proportional to gravimetric Fe contents (Table 3-3) because varying amounts of secondary xylem affected root bulk density, particularly in the lower-order tips.

Iron deposits and internal air space

Hand-cut sections from the distal ends of several 0- and 1-order roots (within 3 cm of apices, 2 mm diam.) were examined microscopically after some colored components were removed by heating in concentrated NaOH. Secondary xylem produced by the incomplete cambium first occurred 2 to 3 cm behind the apices (Figure 3-3). Remnants of the primary cortex were still evident even after a complete cylinder of secondary xylem appeared. A yellowish-red precipitate not affected by NaOH encapsulated most cortical parenchyma cells (Figure 3-4a). When decalcified, the cells collapsed forming hollow yellowish-red casts (Figure 3-4b), indicating that

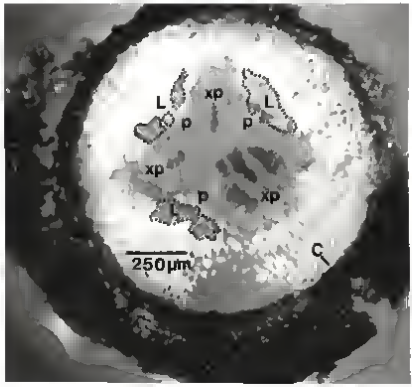
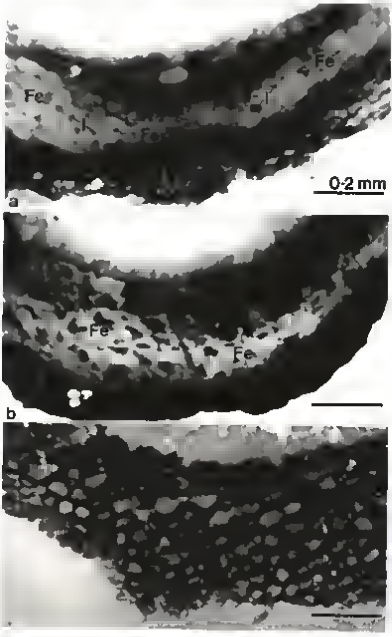



Figure 3-3. Hand section of triarch taproot of slash pine about 25 mm from the apex. Study I. Early stages of secondary growth are evident. Air-filled lacunae (outlined with dots) occur external to the phloem along bows formed by the primary xylem poles. L, lacuna; p, phloem; xp, primary xylem pole; C, cortex.

Figure 3-4 Cortex of triarch slash pine taproot: Study I. (a) After treatment with hot NaOH, showing parenchyma cells densely coated with yellow-brown iron precipitate and network of intercellular spaces. (b) Same section after air drying. Collapse of cells indicates that precipitates coated, not filled, cells. (c) Another section showing uncoated parenchyma after treatment with hot NaOH, followed by dilute HCl to remove iron. Fe, iron precipitate coating cells; I, intercellular space.


Fe
Fe
Fe
0·2 mm
a
Fe
Fe
b

precipitates coated the cell walls rather than filling the interiors. Treatment with 10% HCl dissolved the precipitates, exposing the framework of cortical parenchyma cell walls (Figure 3-4c)

Sequential sections also revealed longitudinal lacunae within the steles of roots (Figure 3-3). The large air spaces occupying >50% of the apical zone of some taproots were continuous with lacunae formed on either side of the primary xylem poles of diarch roots (1- and higher-order roots), or between the bowlike triarch poles of 0-order roots. As the cambium developed between primary xylem and phloem, and secondary growth advanced, centrifugal growth compressed and eventually obliterated the lacunae. As shown in Figure 3-4a, considerable intercellular air space was present among the Fe-encapsulated parenchyma wherever the cortex was intact.

Study II: Mature Trees

Presence of Fe(II) in the Btg, indicating a reducing environment, was revealed by the pink color reaction of ortho-phenanthroline solution applied to freshly exposed subsoil. The entire Btg was strongly reduced near the middle of the shallow depression (Figure 3-1). At the pond margin, the reaction was generally weak in the upper Btg but increased with depth. Within only 15 cm of the upper-Btg1 boundary (Table 3-1), however, a distinct bluish-gray halo, which produced an intense response to the dye, defined a

strongly reduced region, extending 10 to 15 cm outward from a 3 cm diameter taproot of a dead cypress sapling.

Iron contents of high chroma rinds and sheaths

Iron-rich high-chroma precipitates (hues 2.5 to 7 5YR) cemented sand to the surfaces of sinkers (3 to 15 cm diam.) and smaller root branches growing in the low-chroma subsoil (Table 3-4). Likewise, high-chroma precipitates entirely ensheathed some very fine to coarse pine and cypress roots excavated from the root-system pits. Oxidation at 550 C reduced the rinds of high-chroma material on pine sinker roots to sand and bright-red Fe oxide. A 4.3 $cm^2$ area of bark with a strongly cemented 2 mm thick red rind consisted of 56% sand and 2.2% Fe (Table 3-4, 20-100 mm). Although this portion of root was clearly Fe oxidizing, it was only a few centimeters distant from the gleyed zone around the dead cypress root. Root diameter, obviously, did not correlate with gravimetric Fe contents. The Fe-rich rinds coated most surfaces of very-fine and fine slash pine roots in the E and Btg horizons, but on woody sinkers and taproots, the rinds were usually patchy or localized. The most strongly developed rinds (thick, yellowish-red to red, and strongly cemented) seemed to form around bases of emerging rootlets, over basal root surfaces with lenticels, and on the distal ends of sinkers and their multiple branches.

Thick rinds had not formed about the cypress roots examined. Rather, strong-brown to yellowish-red

Table 3-4 Total iron contents expressed in terms of sample mass and the associated root surface area, and the mass loss on ignition (LOI) for pine and cypress roots <2 mm diameter and for high-chroma rinds scraped from larger roots. All are from Btg horizons except as noted. Study II.

| Root | Pine | | | Cypress | | |
|---|---|---|---|---|---|---|
| Diam. | Total Fe | | LOI | Total Fe | | LOI |
| mm | g $kg^{-1}$ | g $cm^{-2}$ | % | g $kg^{-1}$ | g $cm^{-2}$ | % |
| < 2 | 22 | 6.5 | 98 | 41 | 2.6 | 96 |
| | | | | 77 | 2.6 | 88 |
| 2-10 | 7[a] | - | - | 59 | 8.2 | 94 |
| | 44 | 6.9 | 54 | 88 | 3.6 | - |
| | 58 | 11.3 | 94 | 89 | - | - |
| 10-20 | 23 | 1.3 | 98 | 78 | 3.6 | - |
| 20-100 | 22 | 1.3 | 44 | - | - | - |
| | 32 | - | - | - | - | - |

a Uncemented, loose sand rind in E horizon.

preclpitatee (hues 5 to 7 5YR) were depoelted at and wlthln the rhytldome (Table 3-4).

Extractable iron in matrix soil, neoferrans and rinds

The dlthlonlte-citrate-bicarbonate (DCB) buffer extracted crystalline and amorphoue forms of Fe oxlde. It yieided an average of 6.2 g Fe $kg^{-1}$ for neoferrane from the E and Btg horlzone, about 7 tlmee the average content of the eurroundlng eoil matrlx (Table 3-5). Wlth one notable exception, the DCB-Fe contente of eix air-drled rlnde of elaeh plne roots were generally lower than for the neoferrans. The three yellowish-red rlnds from elnkers near the E/Btg boundary were loose eandy materlale, unllke the etrongly cemented neoferrane of the E horlzon. Dlthlonlte-extractable Fe in the two yellowish-red rlnds from the Btg wae eimilar in amount to that ln neoferrane, about one-fourth the total Fe ln other rinde (Table 3-4). For thethird Btg rind in Table 3-5, the DCB Fe content wae elmllar to total Fe contents ln other rlnde (Table 3-4), and wae 75% of the total Fe meaeured ln the eame eample (32 g $kg^{-1}$). Theee high Fe rinds all included a relatlvely high proportion of rhytidome, lndicated in Tablme 4 and 5 by lose on lgnltlon values $\geq$44%

There waa no general relatlonehlp between total P and DCB Fe (Table 3-5). Total-P dietributlon for matrlx, neoferrans and rind eamplee wlthout lerge lncluelon of root rhytldome correlated with %LOI for ($r^2$ = 0.71, n = 31). The concentration of total P verled between 0.09 and 0.14% ww of

Table 3-5 Mean dithionite-extractable (DCB) Fe (± s.d.), total P and loss on ignition (LOI) of matrix soil and neoferrans, and rinds proximal to slash pine sinkers in E and Btg horizons (oven dry weight basis) Study II.

| Material | DCB-Fe | Total P | LOI | |
|---|---|---|---|---|
| | g $kg^{-1}$ | mg $kg^{-1}$ | % | |
| Matrix | | | | |
| E | 0.9( 0 ) | 5.7(0.2) | 0.4(0.1) | (n=2) |
| Bt | 0.8(0.3) | 31.0(1.0) | 3.3(0.2) | (n=4) |
| Neoferrans | | | | |
| E | 5.7( 0 ) | 8.8( 0 ) | 1.0(0.8) | (n=2) |
| Btg | 6.4(0.5) | 33.8(3.5) | 3.0(0.4) | (n=4) |
| Rinds | | | | |
| E/Btg | 3.4(1.2) | 19.7(12.7) | 2.3(0.5) | (n=3) |
| Btg | 5.3(0.1) | - | - | (n=2) |
| Btg | 24.0( - )[a] | 18.0( - ) | 83.0( - ) | (n=1) |

a Rind includes attached rhytidome

the presumed organic fraction (%LOI) for the mineral samples

Acid-ammonium-oxalate (AAO) (pH 4) extracted only amorphous Fe oxide compounds, yielding some 60 to 100% of Fe solubilized by DCB from field moist samples of neoferrans, the Btg soil matrix, and a 3 mm thick sheath surrounding an unidentified root (Table 3-6).

Table 3-6. Comparison of dithionite-extractable (DCB) and oxalate-extractable (AAO) Fe in matrix soil, neoferrans and a high-chroma root sheath. Study II.

| Material | | Fe | | Fe(AAO)/ Fe(DCB) |
|---|---|---|---|---|
| | | DCB | AAO | |
| | | g kg$^{-1}$ | | |
| Matrix | | | | |
| grayish brown | E | 0.9 | 0.7 | 0.8 |
| to light gray | Btg | 0.7 | 0.5 | 0.7 |
| | Btg | 0.7 | 0.7 | 1.0 |
| | Btg[a] | - | 0.6 | - |
| | Btg[a] | - | 1.2 | - |
| Combined Neoferrans | | | | |
| strong brown | Btg | 6.0 | 3.6 | 0.6 |
| to red | Btg | 6.7 | 4.1 | 0.6 |
| | Btg[a] | - | 8.3 | - |
| | Btg[a] | - | 8.6 | - |
| Unidentified-Root Sheath | | | | |
| strong brown | Btg | 20.1 | 11.8 | 0.6 |

a Btg in cypress pond adjacent to mature cypress tree.

## Discussion

### Study I: Saplings

Vertical roots of the central taproot systems of slash pine grew into continuously saturated, anoxic zones of soil. For saplings in study I, the lower two-thirds of vertical extent (29.1 ± 9.7 cm) occurred below the oxidized surface (zone 1) in continuously saturated, non-rust-forming peat (zone 2). These roots were alive when removed after more than 18 mo in the anoxic reduced conditions. The average matrix Eh and pH of zone 2 favored Fe(II) stability (Gambrell and Patrick, 1974; Gotoh and Patrick, 1974) and prevented the formation of Fe oxides from the introduced $FeCl_2$ solution and the formation of rust on steel rods. Calculations indicated that introduction of the $FeCl_2$ raised initial Fe concentrations in the peat near the ends of solution tubes by as much as 80 g $kg^{-1}$. Redistribution and precipitation on roots in the following year, however, decreased concentrations in the peat to between 1.3 and 3.9 g $kg^{-1}$.

Accumulation of Fe oxide on root surfaces is evidence of $O_2$ release and either direct or microbially mediated oxidation of mobile Fe(II) (Figure 3-2, Table 3-3). Roots with associated Fe oxide rinds represented concentrations 6 to 96 times greater than total Fe concentration in the surrounding peat matrix.

The levels of Fe accumulation in small-diameter (<2 mm) roots of slash pine were as great as in flooded-rice roots

(Oryza sativa L.) with Fe oxide coatings (24.3 g $kg^{-1}$, Sacha and Hosaner, 1977; 17.5 to 141.0 g $kg^{-1}$, Chen et al., 1980a). For slash pine, the epidermal and cortical tissues seemed to be the primary sites of Fe oxidation, with the Fe deposits coating external surfaces of most cells in these tissues (Figure 3-4). Occasionally, dead-cell cavities in the epidermis were filled with porous Fe oxide aggregates as observed in the Fe-coated epidermis of flooded-rice roots (Chen et al., 1980b). Smaller amounts of Fe oxide were similarly located in flooded roots of loblolly pine (McKevlin et al., 1987), black spruce, and red pine (Lavan and Rhia, 1986) seedlings. In flooded-rice roots (Green and Etherington, 1977) and bogbean (Menyanthes trifolia, Armstrong and Boatman, 1967), however, the Fe oxide deposits were confined to the epidermis and a few layers of parenchyma in the outer cortex. The oxide-coated cortex was separated from the endodermis by aerenchyma, absent from the cortical tissues of slash pine and other conifers (Coutts and Philipson, 1978; Lavan and Rhia, 1986; Topa and McLeod, 1986b; McKevlin et al., 1987).

Lateral growth of the submerged slash pine roots (note split rhytidome, Figure 3-2) and phloem transport of photosynthates depended on $O_2$ for aerobic metabolism (Crawford, 1978; Coutts, 1982; Hook, 1984). Oxygen thus consumed plus the apparent excess released in rhizosphere oxidation must have been transported through root tissues from the atmosphere. At the distal ends of 0- and 1-order

slash pine roots (presumably also smaller higher-order roots), where primary tissues were still intact, longitudinal gas-filled lacunae in the stele (Figure 3-3) bore striking resemblance to the lacunate steles of flooded-seedling roots of lodgepole pine (Coutts and Philipson, 1978; Philipson and Coutts, 1978) and other southern pines (Topa and McLeod, 1986b). Philipson and Coutts (1978) showed that lenticels on the basal portions of lodgepole pine roots were the chief entry points for $O_2$ which diffused rapidly from the atmosphere, through the stelar lacunae, to aerate submerged roots. For less strongly oxidized roots of flooded-loblolly pine seedlings (Hook and McKevlin, 1988), $O_2$-sensitive electrode measurements detected an internal aeration of the lacunate roots, not observed in non-conditioned, non-lacunate roots.

In the slash pine saplings, however, the lacunate stele provided only a localized transport opportunity in the distal tips of taproots (<5 cm) and higher-order branches. Transport of $O_2$ to tips and provision for leakage from larger-diameter woody roots must be through the xylem or possibly phloem of larger roots. Previous work with deep roots of large slash pine indicated no long-distance transport in the relatively thin phloem, but this possibility was not examined in saplings of the present study. In contrast to the high air-filled porosity, 48 to 69% vv, of the deeper-root xylem (Chapter 2), however, air-filled porosity in the xylem of shallow taproots (1 to 2.5

cm diam ) of the peat-grown saplings was only 15 to 35% vv Thls is the consequence of higher moisture contents in the younger xylem (187% oven-dry weight, s.d 10, 3 samples) as compared with a mean of 87% (s.d. 8) for the deeper sinkers, rather than greater wood substance content. The shallow sapling taproots had a low root bulk density, 294 kg $m^{-3}$ (s d 30) similar to that for the deeper and larger slash pine tap and sinker roots, 260 kg $m^{-3}$ (s.d. 40) Although the volume in which gaseous diffusion can occur in shallow taproot xylem is less than in deeper roots, the maximum distance required for such diffusion is only 55 cm, that is from the peat surface to the tip of the deepest root.

Study II: Mature Trees

In study II, the central taproot and sinker roots of two large slash pines extended to depths of 150 cm or more The lower two-thirds of vertical root extent occurred in subsurface horizons E, Bh, and Btg (Table 3-1) subject to continuous months or years of saturation Reduced conditions resulted in the generally low chroma and gleying of matrix materials, and in Fe segregation.

Fine roots of slash pine, whether extracted from the E horizon or from the gleyed Bt, were generally encased by Fe oxide sheaths The formation of Fe oxide-cemented rinds on larger diameter roots, however, was patchy, and the extent of rind occurrence differed between the two trees On one tree, about one-half of the sinker root surface area had obvious Fe oxide rinds, whereas Fe was much less apparent on

roots of the other tree less than 6 m distant. There were no obvious differences in root system or soil to suggest greater mobility of Fe or greater oxidizing capacity. Within a root system, however, localized rind formation might have occurred in proximity to a concentrated source of Fe(II) (discussed later), or because $O_2$ leakage was more likely from a particular surface. Rinds were often present on surfaces with large lenticels where a smaller resistance to radial $O_2$ diffusion was expected (Hook and Brown, 1972; Phillpson and Coutts, 1978; Topa and McLeod, 1986b). The thickest and most strongly cemented rinds generally occurred around surfaces where branch roots emerged, and at the deep distal ends (<1.5 cm diam.) of sinkers.

Fine roots of pond cypress extracted from the Btg horizons, 60 to 170 cm depth, within two dry ponds and on pond margins in the Austin Cary Forest, and at another site about 5 km distant (Echols, 1983) were all encased by Fe oxide sheaths. The rhytidome of a few medium-sized roots extracted from the Btg was also generally coated by Fe oxides.

Gravimetric Fe contents of rinds were generally greater on cypress than on slash pine roots (Table 3-4). Conversion of total Fe to terms of surface area of root associated with the rind, however, indicated similar areal intensities of oxidation at surfaces of the two species (pine, 1.3 to 11.3 mg $cm^{-2}$; cypress, 2.6 to 8.2 mg $cm^{-2}$, Table 3-4). Total Fe served as an index of localized $O_2$ fluxes into the

rhizosphere for roots growing in similar soil environments. The conversion of data from gravimetric to areal terms showed what was already visually apparent, i.e., that while Fe was concentrated in a relatively small mass of soil and rhyzidome at the surface of cypress roots, the Fe oxide near slash pine roots was less concentrated in mass but extended further from the surfaces. The total Fe accumulation (mg $cm^{-2}$) near roots of both species grown in mineral soil was an order of magnitude greater than for the tips of peat-grown slash pine roots (0.51 ± 0.26 mg $cm^{-2}$), although the gravimetric contents for the peat roots were often greater (sapling 4, Table 3-3). It is not clear whether this was due to a lesser cumulative $O_2$ flux from the roots or to greater $O_2$ consumption by pest processes unrelated to Fe(II) oxidation. Complexation of Fe by organic ligands generally limits Fe oxide formation in organic soils (Schwertmann et al., 1986).

Neoferrans extracted from the bleached E and Btg horizons were Fe oxide accumulations surrounding fine-root pores. Occasionally, pores still contained a root but more often the neoferrans were residues remaining when decay of the root occurred without entirely re-reducing Fe oxide sheaths and other Fe(III) accumulations within the sheath. The DCB Fe extracted from yellowish-red neoferrans (Btg) at the site studied by Echols (1983) was some 6 times greater than for neoferrans extracted from the slash pine pits at

the Austin Cary Forest (Table 3-5). The Echola neoferrans were probably the result of live cypress root activity.

Iron Precipitation and Mineralogy

The Fe accumulated by roots of slash pine and pond cypress was transported from the matrix peat or soil, either by mass flow of water-soluble Fe(II), or by diffusion to regions of lower Fe(II) concentration at root surfaces (Howeller and Bouldin, 1971). Oxygen leaking from the roots reacted directly or indirectly with Fe(II), precipitating Fe(III).

It is probable that initial Fe precipitation was microbial (Schwertmann et al., 1986) although there was no direct evidence to that effect. Ariatovskaya and Zavarzin (1971) reported that Fe-capsule forming bacteria of the family Siderocapsaceae Pribram 1929 (Zavarin, 1974) were important amongst Fe-accumulating organisms isolated from wet soils in swamps. These bacteria apparently utilize the organic portion of Fe-organic complexes and precipitate Fe(III) in or on encompassing soil capsules. Schwertmann and Fischer (1973) characterized the ferric hydroxides deposited by soil micro-organisms as poorly crystalline ferrihydrite.

Ratios of 0.6 for AAO- to DCB-extractable Fe (Table 3-6) indicated a high proportion of amorphous Fe oxide in neoferrans and sheath material (the unidentified root) extracted from the Btg in slash pine root excavation pits. This was also true of channel neoferrans (Echola, 1983) from

the Btg of another Paleaquult pedon. The amorphous materials were most likely ferrihydrite (Schwertmann et al, 1986), which Schwertmann and Fischer (1973) found to be 90 to 100% AAO soluble.

X-ray diffraction patterns of AAO-extracted sand-free fractions of neoferrans and rind materials showed no evidence of crystalline Fe oxide, although W.G Harris (Soil Science Dept., Univ. Fla., pers. comm., 1985) detected low peaks characteristic of goethite in one sample of an oxidized sheath around the unidentified root (20.1 g $kg^{-1}$ DCB Fe, Table 3-6). The concentration threshold for detection of goethite (αFeOOH) and lepidocrocite (γFeOOH) were high, however, because of poor sample orientation. Crystalline FeOOH forms might have occurred undetected because the FeOOH content in the KOH-treated, sand-free fraction of the sheath was still only between 4 and 7% ww.

Lepidocrocite and goethite were detected by X-ray analysis in Fe oxide coatings removed from rice roots (Bacha and Hoosner, 1977; Chen et al., 1980a). According to Schwertmann and Taylor (1977), lepidocrocite is usually associated with hydromorphic soils, being formed by the oxidation and dehydration of Fe(II)Fe(III)-hydroxy salts. Goethite can form from ferrihydrites when additional Fe(II) promotes the dissolution and subsequent slow hydrolysis reactions. Organic and inorganic ions, and $CO_2$ influence the rate and product of recrystallization.

There was no evidence of significant P precipitation within ferrihydrites or FeOOH comprising neoferrans and rinds. Adsorption of P by Fe oxide is well known (Schwertmann and Taylor, 1977), but the mass of Fe deposited on roots is not an indication of the actual P adsorbing surface area. Furthermore, other anions, particularly organic anions in the rhizosphere, might well have a competitive advantage for adsorption sites over the small amounts of P transported into the Fe sheaths. Organic anions can compete with P for adsorption and increase P availability to plants (Hingston et al., 1968).

Iron Cycling in the Root Zone

Figure 3-5 suggests a mechanism for the conservation of Fe in the soil-root system despite the dominance of reducing reactions in the soil matrix. Soluble Fe(II), indicated by reaction with ortho-phenanthroline, occurred throughout the sandy-clay loam subsoil matrix of Surrency sand in close proximity to well developed Fe oxide rinds on root surfaces, or surrounding root-pore mottles (neoferrans). Anaerobic decomposition of dead roots and other organic matter was the source of Fe(III)-reducing potential. The persistence of iron oxide coatings in the upper soil, e.g., as neoferrans, may well occur if periodic drying and air entry allow aerobic rather than anaerobic decomposition. The presence of neoferrans at depth, however, indicated that the yield of Fe(III) reducing potential by anaerobic decomposition was commonly less than the reducible Fe in fine root sheaths.

Iron, thus solubliised, would be transported laterally, as well as vertically, by mass flow or diffusion processs Distances between roots are small within the central root system of slash pine, and it is easy to visualize Fe(II) mobliised by a dead root being re-oxidised and precipitated on a neighboring live root

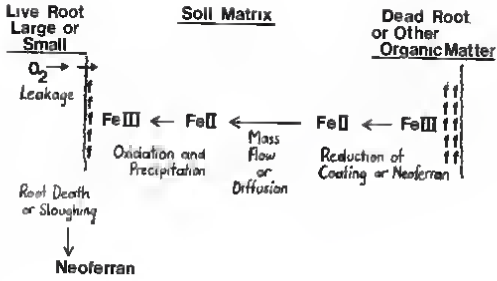



Figure 3-5. Model for the conservation of iron in the root-soil system. Decomposition of dead roots and other organic matter reduces oxidized iron, Fe(III), to mobile Fe(II) which is transported through the soil matrix to oxidizing live root surfaces, where Fe(III) is precipitated. Neoferrans remain after small roots die and decompose.

# CHAPTER 4
# ACTIVE K-UPTAKE BY SLASH PINE FROM $O_2$-DEPLETED SOLUTIONS

## Introduction

Slash pine (Pinus elliottii Engelm var. elliottii) growing on flatwoods and coastal savanna soils of the southeastern United States encounters shallow water tables that severely reduce soil-$O_2$ supply to large parts of the deep root systems. As much as one-third of the fine root length may occur below 100 cm depth (Van Rees and Comerford, 1986), yet water tables commonly rise to within 50 cm of the soil surface (Pritchett and Smith, 1974; Kaufman et al., 1977; Riekerk et al., 1978). Tap and sinker roots grow as much 90 cm into soil that is only rarely unsaturated (Schultz, 1972 and 1973).

The presence of a longitudinally continuous air-filled pore space through large-diameter roots of slash pine was demonstrated in Chapter 2, suggesting that long-distance $O_2$ transport enables submerged roots to grow and function aerobically during extended periods of inundation. Uptake of nutrients depends on aerobic metabolism to produce high energy potentials within cells and to maintain active uptake processes (Mengel, 1974; Clarkson, 1984). Topa and McLeod (1986a) suggest that the absorption of phosphorus from

anaerobic solutions by loblolly pine (Pinus taeda L.) and pond pine (P. serotina Michx.) seedlings is an aerobic process associated with enhanced internal aeration.

In the present study, we investigate the hypothesis that, in slash pine, $O_2$ is transported internally from the stem and roots above the water table to the submersed root system in sufficient amounts to support aerobic root function. In other flood-tolerant woody species, internal $O_2$ transport to roots has been shown either by varying the gas composition of the atmosphere surrounding foliage, stem or basal roots while observing radial $O_2$ leakage from lower roots immersed in a deoxygenated medium (Armstrong, 1968; Armstrong and Read, 1972; Hook and Brown, 1972; Phillipson and Coutts, 1978, 1980), or by directly observing $O_2$ concentration within roots (Hook and McKevlin, 1988). In the present study, we use the absorption or leakage of K to indicate treatment effects on the aerobic function of roots bathed in micro-aerobic solutions. Although K is actively absorbed by roots, it also diffuses passively across cell membranes in the direction of decreasing electro-chemical potential (Mengel, 1974). Treatments that decrease aerobic respiration immediately reduce active uptake processes, resulting in a net efflux or leakage of from roots.

## Methods and Materials

Fifty 1-0 slash pine nursery seedlings with long taproots were lifted and established in vertically divided root-system units (Figure 4-1). The upper chambers were 26 L pots filled with 4:3 peat:pearlite (vv) mixture. The lower solution chambers were 1 m lengths of 10.2 cm i.d. PVC pipe capped at both ends and filled with 2 mM $CaCl_2$. The seedlings were planted deeply, and the taproots led through 3.5 cm i.d. tubes that protruded from the pot bottoms 3 cm into the solution chambers. Within the tubes, a collar of foam rubber filled the space around each taproot. After 21 months, however, these tubes were constricting taproot growth and were removed.

Each solution chamber was fitted with two access ports. The upper, about 5 cm below the chamber top, was attached through a shared pipeline to a constant level cistern that supplied 2 mM $CaCl_2$ in deionized water. During the initial 23 months the water was equilibrated with air.

The units were placed in concrete-walled trenches, the pots seated on rails at ground level with the solution chambers extending below. The tops of the trench including the pots were enclosed with urethane insulating board to reduce daily and seasonal temperature fluctuations.

Concentrated superphosphate (1 g P/sapling) was combined with the peat-pearlite mixture at planting, and macro-nutrient solutions were applied to the upper-root chambers periodically thereafter. Each sapling was given a

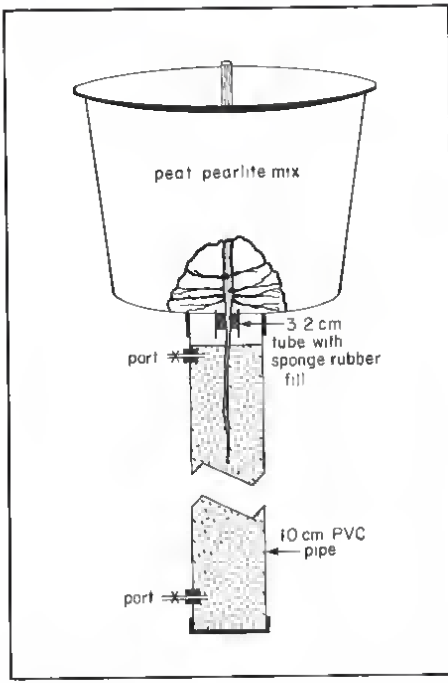



Figure 4-1 Two-chambered root-system unit: the upper chamber is a pot containing well-drained peat-pearlite mix where the basal taproot and branching laterals developed; the lower chamber is a 1 m long cylinder containing 2 mM $CaCl_2$ solution where the distal tap and sinker roots developed.

total of 3 g K in two applications at 12 and 15 months, after which K was omitted from the macro-nutrient solutions. Micro-nutrients were added once. Each pot was watered at frequent intervals and excess rain excluded with a polyethylene skirt secured around the stem base.

Conditioning Roots

After 23 months, sixteen seedlings with strong taproots 30 to 40 cm below the pot bottoms were moved to half-length solution chambers. They were then subjected to micro-aerobic conditions for the following 5 months as indicated in Table 4-1. Compressed $N_2$ was forced through a glass sparger at the bottom of each solution chamber to displace dissolved $O_2$ and volatile metabolic products. For the first two months the solutions were sparged only once each week until dissolved $O_2$ levels were <0.5 ppm $O_2$. For the next three months, the solutions were sparged continuously at a low flow rate, maintaining a small positive pressure of $N_2$ in the 5 cm long headspace surrounding the entering taproot. $N_2$ bubbles agitated solutions.

Each solution chamber was attached to an individual 2 L Mariotte vessel. Measured periodic reductions in the Mariotte solution corresponded to cumulative water uptake by the lower-chamber roots. The Mariottes were refilled daily, or when depleted, with $CaCl_2$ solution that had been sparged with $N_2$. Slowly permeable Mylar balloons filled with $N_2$ gas were attached to air-inlets of the Mariottes thus retarding aeration of contained solutions.

Table 4-1 Schedule of sapling treatments.

| month | |
|---|---|
| 0 | 1-0 seedlings planted in divided root-system units. |
| 21 | Tubes constricting taproots removed. |
| 23 - 25 | Root conditioning of 16 saplings begins. Solutions sparged with $N_2$ once/week. |
| 25 - 28 | Root solutions continuously $N_2$ sparged. |
| 28 - 29 | Saplings ranged in height from 1.0 to 1.7 m. Experiments 1 to 5 initiated, each using six pre-conditioned saplings. |
| 30 | Experiment 6, with 12 pre-conditioned saplings. |
| 30 | Experiment 7, with 6 treatment saplings of Experiment 6. |

Measuring Dissolved Oxygen

Dissolved oxygen concentrations in solution samples were measured using a Yellow Springs Instrument (YSI) portable oxygen meter and membrane-covered polarographic probe. Samples withdrawn from continuously sparged root-bathing solutions ranged from 0.2 to 0.5 ppm $O_2$, suggesting that the equilibrium gas atmosphere contained from 0.5 to 1.2% $O_2$ vv at 25 C. The sparging $N_2$ contained <0.001% $O_2$ vv. Moreover, placing the probe directly in a sparged solution with no root system indicated 0 ppm $O_2$. Hence, the higher levels observed in the sampled solutions were due either to contamination when withdrawing samples or to $O_2$ diffusing from the root systems.

K-Uptake Experiments

At 28 months (Table 4-1) the saplings ranged in height from 1.0 to 1.7 m and from 5 to 6 cm in stem diameter (outside bark) just above the soil surface. Prior to beginning each K-uptake study, the root-bathing solutions of pre-conditioned saplings were replaced with fresh $CaCl_2$ solution and the roots were allowed to adjust for at least 2 days with continuous $N_2$ sparging. At the start of each experiment, 150 $cm^3$ solution samples were withdrawn and analyzed to establish initial K concentrations. Then, 200 μmol K as KCl was added to raise concentrations to about 50 μM. Solution sampling was repeated 10 to 20 minutes after K addition and at various intervals thereafter. The

Mariotte vessels supplied $N_2$-sparged deionized water in response both to sample removal and sapling transpiration.

Solution samples were concentrated 5- to 10-fold and analyzed by atomic emission spectroscopy with 0.2% Cs to suppress ionization. Periodic K-uptake was calculated by difference, accounting for the dilution caused by sample withdrawal.

Experiments 1 to 5

K-uptake by six pre-conditioned saplings was investigated in five consecutive experiments. In Experiments 1 to 3 the solutions were kept micro-aerobic. In Experiment 4, the sparging gas was changed to air for 10 days while K-uptake was monitored. The root systems were then examined, solutions changed, and $N_2$ sparging resumed for Experiment 5.

Experiment 6

Previously measured K-uptake rates, water use and appearances of lower root systems served as the basis for allocating twelve pre-conditioned saplings (including the six saplings used for Experiments 1 to 5) to two similar groups that were randomly assigned to treatment. Each sapling pot (upper root chamber) was then enclosed in a double thickness of 0.03 mm polyethylene bags. In the case of treated saplings, the bags were secured around stems just above the soil and around the lower chamber just below the the junction of pot and cylinder. Air was expelled from the closed bags by slowly flowing $N_2$ gas. Three hours later,

near sunset, the whole crowns and pots of both treated and control saplings were enclosed within two joined 0.04 mm polyethylene trash bags. These covers were loosely tied around the control saplings, allowing free air exchange. With the treated saplings, however, the bags were secured below the pot-cylinder junctions and inflated with slowly flowing $N_2$ gas, which entered through a tube at the bottom and exited through an opening at the top throughout the night.

Meanwhile, $N_2$ sparging kept root-bathing solutions of all saplings micro-aerobic. Root solutions were first sampled 1.5 hours after enclosing the pots, and K addition and uptake measurement began 3 hours after crown enclosure (Figure 4-4). A heavy cloud cover allowed the enclosure period to extend to mid-morning. The bags were removed 17.5 hours after enclosure and the solutions were sampled again. Additional solution samples were taken one and four days later.

Experiment 7

After a 10 day recovery period, the six treated saplings of Experiment 6 were randomly assigned to treatments in a longer-term enclosure experiment. For each sapling, the upper root system and the basal stem (about 15 cm buried in the soil medium plus 10 cm above the soil surface) were again enclosed in plastic bags. For 6 days, the bags of three controls were open to air while $N_2$ gas flowed slowly through the bags of three treated saplings to

produce an $O_2$-free $N_2$ atmosphere. With continued $N_2$ sparging of root-bathing solutions, K-uptake studies began 4 hours after enclosing the pots (Figure 4-5). Solutions were sampled periodically for 5 days, and then twice again after the $N_2$-filled bags had been opened to air.

## Results

### Saplings and Lower Root Systems

The saplings used in this study were similar in respect to root system and crown development. The upper soil chamber contained about a 15 cm length of basal stem (buried), a 15 cm length of taproot, and branching lateral roots. The lower root systems filled the solution chambers to a depth of about 40 cm (Figure 4-2).

Taproots were 4 to 7 cm in diameter just below the pot-cylinder junctions but commonly divided into two or several major branches (sinkers) at least 1 cm in basal diameter. These 0-order roots, up to 20 cm in length, tapered slightly to their distal ends. The original tips were often replaced by 2 or 3 short, prongiike adventitious branches, about 0.4 cm in basal diameter. Secondary xylem formation progressed to within 1 cm of the root apices (about 0.2 cm in diameter).

The many first-order branches were relatively short (<15 cm in length) and woody, ranging from 0.1 to 0.7 cm in basal diameter. Whereas the 0-order roots were characteristically triarch or tetrarch with branches


Figure 4-2. A lower-chamber root system maintained in micro-aerobic solutions for 7 mo, including the experimental period. The taproot was about 5.7 cm in diameter where it emerged from the upper chamber and divided into at least two 0-order branches (O). Several prongiike adventitious branches (A) replaced the original 0-order root tips. Many 1-order branches (1) exhibited growing white tips and diarch branching patterns that subtended at least two further branching orders. The vertical bar is equivalent to 10 cm length.

originating around the circumference, branching from the 1- and higher-order disrch roots was generally two-ranked. The 2- and 3-order roots, rarely more than 2 cm in length, lent a brushy appearance to the solution-root systems. These very fine roots (≤1 mm diameter) comprised the main absorbing root length, averaging 101 ± 36 m/sapling (mean ± s.d.) at the time of treatment.

In the late summer and autumn when K-uptake studies were conducted, the very fine roots had short white tips usually <1 cm in length, indicating slow root extension in spite of the micro-aerobic condition.

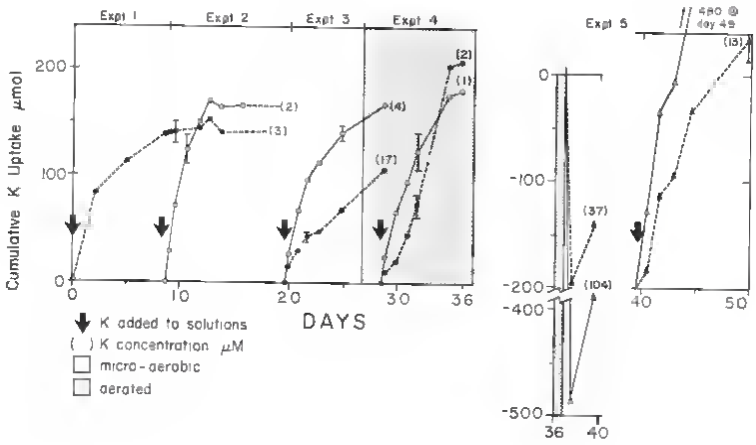
Experiments 1 to 5

Prior to beginning these experiments, no K had been added to the micro-aerobic solutions bathing the lower-chamber root systems. Apparent losses from the roots established equilibrium concentrations of 2 µM K. At the beginning of Experiments 1 to 3, or some time thereafter for Experiments 4 and 5, solution concentrations were adjusted to about 50 µM K, except where untreated saplings were retained as controls. In each case, the initial value corresponds to the zero cumulative uptake datum in Figure 4-3.

K-uptake from micro-aerobic solutions

At the beginning of Experiment 1, the solution K concentrations for three saplings (Group 1) were raised to 48 µM K while three similar saplings (Group 2) with no added K served as controls. On day 9, solution K concentrations

Figure 4-3 Average cumulative uptake or efflux of K by slash pine seplings subjected to a continuous sequence of treatments. Ordinal values reset to zero at each addition of K (arrows) and at each change from air sparging to $N_2$ sparging of solutions. Experiments 1 to 4: lines represent two groups of three seplings, group 1 (●) and group 2 (○). Experiment 5: the same six seplings were divided into a group of four (▲) and a group of two (△) (see text). Parenthetical values are the average solution-K concentrations (μM) at the end of each treatment. Mean temperature 26 C. Vertical bars are maximum standard errors for each curve.


Expt 1
Expt 2
Expt 3
Expt 4
Expt 5
Cumulative K Uptake μmol
200
100
0
-100
-200
-400
-500
0
10
20
30
36
40
50
DAYS
(2)
(3)
(4)
(17)
(1)
(37)
(104)
(13)
480 @ day 49
K added to solutions
( ) K concentration μM
micro-aerobic
aerated

for the Group 2 seedlings were also increased to 48 uM K (Experiment 2). Both groups depleted solutions of K with the average cumulative K-uptake (μmol K) increasing curvilinearly toward approximate plateaux corresponding to solution K concentrations of 8 μM K in 9 days (Group 1, Experiment 1) or 5 μM K in 4 days (Group 2, Experiment 2). By day 20 most seedlings had reduced solutions to 2 μM K. Removal of larger solution sample volumes in Experiment 1 reduced the total amount of K available for uptake by Group 1 seedlings, and thus reduced their cumulative uptake as compared with Group 2 seedlings.

To begin Experiment 3, solution K concentrations for both groups were increased simultaneously to 52 μM K. Group 2 seedlings absorbed K much more rapidly than Group 1 seedlings, indicating that the different uptake rates in Experiments 1 and 2 were not merely artifacts of treatment date. Because the two groups were formed by random assignment of comparable seedlings, the difference in mean uptake rates could not be attributed to any obvious seedling features.

K-uptake response to solution aeration

Experiment 4 began when the sparging gas was changed from $N_2$ to air (day 25) before seedlings had fully depleted the K added for Experiment 3. Although the solutions were rendered nearly air-saturated within a few hours, solution samples removed 2 days later did not indicate an immediate effect of aeration on the average K-uptake rate. Later,

after solution K concentrations had been raised to 63 μM K (Group 1) or 52 μM K (Group 2), the rates of K-uptake increased with time even as solution K was depleted. In the previous three trials, K-uptake rates had decreased with depletion of solution K. The aeration response, more notable with Group 1 saplings, probably correlated with a period of rapid root elongation. Another preliminary experiment showed that, although new apical growth began immediately, rapid elongation lagged a few days behind the change from $N_2$ to air sparging; in Experiment 4, first-order root apices grew 3 to 10 cm in length, and higher order roots grew 0.1 to 3.0 cm during 10 days of aeration.

Response of aerated roots to micro-aerobic solutions

Experiment 5 began with the resumption of $N_2$ sparging. Within 17 hours, dissolved $O_2$ concentrations were reduced to below 0.5 ppm, and the new white root tips generated during the aerated period had discolored and lost turgidity. The fresh bathing solutions became unusually turbid, presumably from organic substances released by the stressed roots and an accompanying flush of microbial growth. The $N_2$ exhaust from the lower chambers carried a "sweat" organic odor.

Concurrently, total K contents of the bathing solutions increased to between 180 and 490 μmol, indicating K leakage from the stressed root systems. To accommodate these large effluxes, the datum in Figure 4-3 is elevated between days 36 and 40. Individual saplings were also regrouped: four saplings with lesser efflux (average 180 μmol K) and two

saplings with greater efflux (average 490 μmol K), measured 17 hours after $N_2$ sparging resumed.

By the third day in micro-aerobic solutions, however, all root systems were maintaining net K-uptake. At that time, the addition of about 50 uM K increased concentrations to 80 μM K (for the lesser-efflux saplings) and 154 μM K (for the greater-efflux saplings) to begin new cumulative uptake curves. The subsequent K-uptake rates were higher than during Experiments 1 to 3, which began at lower initial K concentrations. After 10 days, when the experiment ended, saplings had reduced solution concentrations to an average of 13 μM K (range 6 to 35 μM K).

Experiment 6

Experiment 6 began in the mid-afternoon (0 h, Figure 4-4) when plastic bags surrounding the pots and basal stems of treated saplings were first inflated with $N_2$. Some closure-induced efflux of K from the solution roots was apparent 1.5 hours later. This K-efflux raised the average solution concentration for the six treated saplings to 14 ± 13 μM K. Conversely, the concentrations in micro-aerobic bathing solutions for the six control saplings (bags open to air) remained at 4 ± 2 μM K.

Beginning near sunset (3 h, Figure 4-4), bags enclosing the entire plant (tops plus pots) of treated saplings were flushed continuously with $N_2$. $O_2$ was depleted to 6% (vv) after 3 hours of enclosure, and was negligible by the

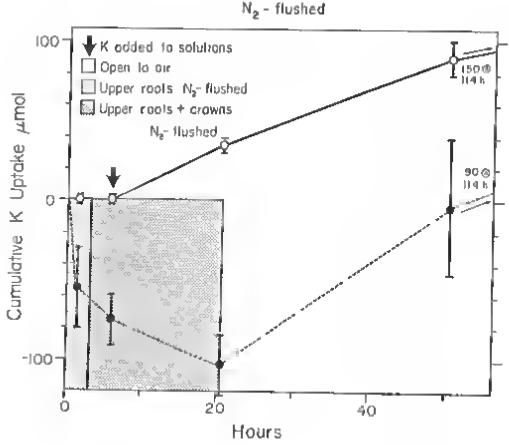



Figure 4-4. Average cumulative K uptake or efflux by sapling roots in $N_2$-sparged solutions (~21 C) when upper roots and top remained open to air (O , n=5), or when only upper-root systems, followed by both upper roots and whole crowns, were enclosed for a time in $N_2$ flushed bags (● , n=4). Shading shows the duration of $N_2$-exposure. Vertical bars indicate standard errors of the means.

following morning (20.5 h). The K-uptake experiment was initiated after 3 hours of crown enclosure (6 h, Figure 4-4) by raising the average solution concentration of five control saplings to 48 ± 4 μM K and of four treated saplings to 67 ± 9 μM K. Data from only these saplings comprise Figure 4-4 because the Mariottes for three other saplings malfunctioned. Qualitative treatment effects for the three remained valid, however.

Slow K-efflux from the solution roots further increased K concentrations in micro-aerobic solutions for all six treated saplings. After 17.5 hours of whole-crown enclosure (20.5 h, Figure 4-4), the average solution concentration for the four saplings with functioning Mariottes was 74 ± 12 μM K, indicating the average negative uptake (efflux) of -28 ± 14 μmol K. Five control saplings, on the other hand, depleted solutions to 39 ± 3 μM K in the same period, absorbing 35 ± 13 μmol K while doing so.

Solution samples taken 30 hours after enclosure removal (50 h, Figure 4-4) reveal the rapid recovery of K-uptake. Within 4 days of bag removal, the treated saplings reabsorbed about two times their average total efflux of 105 ± 44 μmol K, reducing solution concentrations to 14 ± 9 μM K. Control saplings depleted solutions to 8 ± 5 μM K in the 4.5 days following the addition of K. Given more time, all saplings probably would have established their previous steady-state K levels.

Temperatures in the crown bags (both $N_2$-flushed and open) were 13 C at 9 h (Figure 4-4) and remained near this value throughout the night. As the morning clouds cleared, temperatures then increased rapidly to 32 C before the bags were removed at 20.5 h. Ethanolic odors in the exhaust gas of the $N_2$-inflated crown bags indicated that anaerobic fermentation had occurred. Although the crowns in general were not damaged by the anoxia or the higher temperatures, varying lengths of the needle tips on recent growth flushes, particularly in the $N_2$-inflated bags, were discolored, appeared resin-soaked, and eventually died.

Experiment 7

In Experiment 7 (Figure 4-5), solution-chamber roots of the three saplings sustained slow K-effluxes as long as bags enclosing the pots and lower stems were being flushed with $N_2$ gas. The anoxia-induced K-efflux was sensitive to interruptions in $N_2$ flow through the bags, however. Between samplings 2 and 3 (days 1 and 2), gas flow stopped for several hours, and air exchange temporarily increased $O_2$ concentrations in the enclosures. Concurrently, K-efflux decreased but then increased to previous levels after $N_2$ flow resumed and $O_2$ was again depleted. The total K-efflux in 6 days (60 to 100 μmol K) was only as great as the average efflux resulting from 20.5 hours total crown enclosure in Experiment 6. Meanwhile, three control saplings depleted their micro-aerobic root bathing solutions of added K.

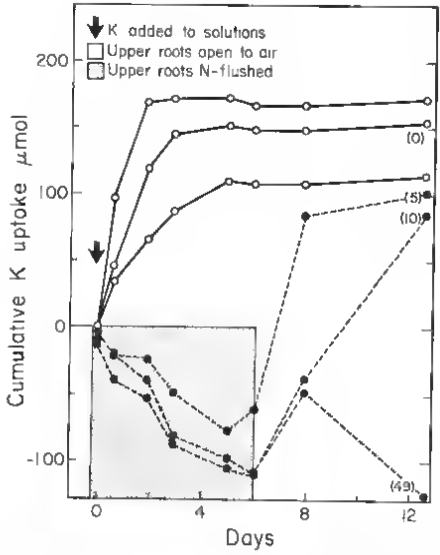



Figure 4-5: Average cumulative K-uptake or efflux by sapling roots in $N_2$-sparged solutions (~10 C). Upper roots of three control saplings (○) remained open to the air throughout. Upper roots and lower stems of three treated saplings (●) were enclosed in $N_2$-flushed bags for 6 days, then opened to air once more. Measurable $O_2$ was present in the bags at approximately 2 days but not thereafter. Parenthetical values represent terminal K concentrations (μM).

After removal of the enclosures (day 6), solution roots of two treated saplings reabsorbed K from micro-aerobic solutions at rates comparable to those of the control saplings. By day 13, these two saplings had depleted solutions to 5 and 10 μM K. The solution roots of a third sapling, which failed to sustain net K-uptake, were brown and limp to the tips.

K-Uptake and Mass Influx

Slopes of the cumulative K-uptake curves (instantaneous K-uptake rate) decreased as solution K concentrations were depleted (Figure 4-6). Moreover, the relationship between average K-uptake rate and solution K concentration differed in repeated experiments even with the same saplings (Group 2 saplings, Experiments 2 and 3)

Since water intake over time for each sapling was measured in all experiments, the mass K-influx (i.e., water absorbed per water-uptake period x average solution concentration) was compared with the total periodic intake of K (Figure 4-6). The mass-influx estimate was generally smaller than the total K-uptake, and the difference was presumed to be a minimum estimate of active K-uptake by the solution roots. Differences between total and mass influx were, however, greatly affected by the time of day in which the uptake interval fell, and by climatic factors. The first intervals of both Experiments 2 and 3 spanned only high evapotranspiration (ET) daylight hours (900 to 1800 h). Thus, high water use and high initial K concentrations

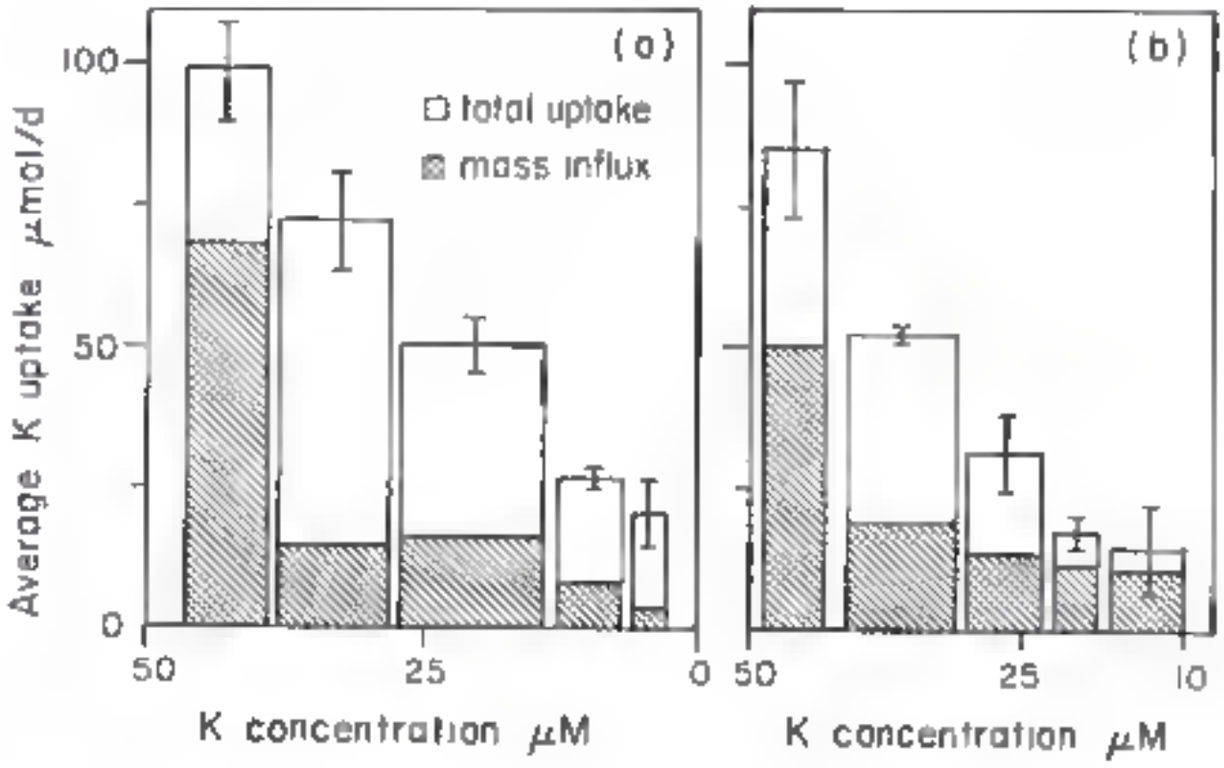



Figure 4-6 Comparison of the total periodic K uptake and mass influx for Group 2 seplings in Experiments 2a and 3b Histogram bars show the average concentration range for each sampling period, with sample withdrawal producing small decreases between periods Vertical bars indicate standard errors of the means.

yielded maximum estimates of mass influx, on the order of 60 to 70% of the total K-uptake. Subsequent sampling intervals spanned both night and day, resulting in lower water use for the period and in mass-influx estimates that were generally less than half the maximum K-uptake rates. In Experiment 3, total K-uptake converged with the estimated mass influx (for solutions <25 μM K), but the data do not distinguish between active uptake during minimum water use intervals and uptake during periods of high water use.

Normal K-uptake rates occurred during sample intervals of relatively low water use in Experiments 6 and 7 (Table 4-2). Mass influx accounted for only 20% of the total overnight K-uptake in Experiment 6. Heavy cloud and cool temperatures during the first 3 days of Experiment 7 caused low water consumption; consequently, mass-influx estimates for the control saplings represented only 6.2, 6.7 and 12.5% of the total K-uptake for the three periods shown in Table 4-2. Thus, roots in micro-aerobic solutions absorbed K by active processes at concentrations even as low as 0.5 μM K (Experiment 7, 1.9 - 2.8 days).

Table 4-2 Comparison of total periodic K-uptake rates and mass influxes of K for the 5 and 3 control saplings in Experiments 6 and 7, respectively, during low water-use periods, 0.21 ± 0.11 L day$^{-1}$ (Exp.6) and 0.21 ± .04 L day$^{-1}$ (Exp 7)

| Exp no. | Sample period | Average periodic solution conc.[a] | Average K-uptake rate total | mass influx |
|---|---|---|---|---|
| | day | μM K | μmol day$^{-1}$ | |
| 6[b] | 0.0-0.8 | 44±3 | 44±16 | 9±5 |
| 7[c] | 0.0-0.6 | 32±6 | 97±55 | 7±1 |
| | 0.6-1.9 | 16±5 | 45±18 | 3±1 |
| | 1.9-2.8 | 6±5 | 16±13 | 1±1 |

a Mean ± s.d.
b Period includes overnight and overcast morning.
c Heavy cloud and cool solution temperatures, reduced from 17 C to about 11 C, caused low water use.

## Discussion

Healthy slash pine roots were maintained in micro-aerobic solutions for 5 months. Dissolved $O_2$ levels in these solutions were about 0.5 ppm $O_2$ (equivalent to 1.2% vv $O_2$, 25 C), although it is unclear whether this concentration solely represents leakage from the roots or includes contamination during withdrawal of solution samples.

Saplings absorbed water from lower solution chambers. The maximum uptake rates, about 1 $dm^3\ d^{-1}$, occurred in midsummer while water was excluded from the upper chamber. If the sapling crown projection areas were of the order of 0.5 and 1 $m^2$, then this water use represents a transpiration loss of 1 to 2 mm $d^{-1}$. Thus, roots in micro-aerobic conditions could have met as much as one-half the potential evapotranspiration (4 mm $d^{-1}$, June to August) estimated by Hammond et al. (1981). The fine-root length in solutions seemed great enough to sustain such an evaporative demand, but estimates of hourly water absorption on a total fine-root surface-area basis, averaging on the order of 10 $mm^3\ cm^{-2}\ h^{-1}$ (from 24 h water use data), were low in comparison with actual measurements for suberized roots of loblolly pine seedlings (Chung and Kramer, 1975).

### $O_2$ Supply, Root Function, and K-Uptake

Since K-uptake is an $O_2$-dependent process, it serves as a measure of how well aerobic root function was maintained in a micro-aerobic medium. For roots bathed in dilute solutions (<100 μM K), active membrane transport

(respiration dependent) maintains high K concentrations inside the cells, against electro-chemical gradients that would otherwise cause K diffusion out of roots (Cheeseman and Hanson, 1979; Clarkson, 1984). Although there is normally some passive K diffusion out of cells, its rate is considerably less than the concentration-dependent active uptake, except in very dilute bathing solutions. In such solutions, on the order of 1 to 3 μM K, a steady state between active K-uptake and K-efflux occurs (Mengel, 1974).

Sudden $O_2$ deprivation, however, results in large net efflux of K. Active transport ceases, and K diffuses from the concentrated internal solutions into considerably more dilute bathing solutions. Plum roots, for instance, leaked K into bathing solutions within one hour of changing from air to $N_2$ sparging (21 to 1% vv $O_2$) (Rosen and Carlson, 1984). After 18 h in micro-aerobic solution, the same roots then resumed net K-uptake immediately after air sparging resumed. This reversible response reflects changes in cell energy level rather than more fundamental damage to cell membranes. If tissue anoxia persists, the permeability of cell membranes increases, as does the likelihood of permanent tissue damage (Crawford, 1978; Hook et al., 1983).

In the present study, pre-conditioned slash pine roots established steady-state concentrations with fresh $CaCl_2$ solutions at about 2 μM K, and reduced KCl-amended solutions from 50 μM K to the same low level (Experiments 1 and 2). These roots absorbed K at rates in excess of mass influx

with water, even from the most dilute bathing solutions (Table 4-2).

Uptake of K occurred against large concentration gradients, from <50 μM K bathing solution into tissues where concentrations averaged 25 to 36 mM K (estimated from total K-content of fine roots in bathing solutions <10 μM K, divided by their water content, for three saplings used in K-uptake Experiments 1 to 6). As calculated from Clarkson (1984), passive diffusion of K into aerobic roots at steady state with bathing solutions of 50 μM K could maintain internal K concentrations at only one-tenth of the levels observed for the fine slash pine roots. Thus, these roots must have absorbed K from micro-aerobic solutions by an active transport process (Bowling, 1976; Clarkson, 1984).

Active uptake processes for pre-conditioned slash pine roots depend on $O_2$ transported from the upper roots and/or sapling stems exposed to air (Experiments 6 and 7). Net efflux of K occurs when $N_2$ replaces air in enclosures surrounding the lower stem and basal roots (Figure 4-4 and 4-5). This effect is reversible. Net uptake of K resumes soon after enclosures are removed or, as in Figure 4-5, when $N_2$ flow is temporarily interrupted. This suggests that root function is responding directly to levels of $O_2$ availability. The larger variability in K efflux when only upper chambers were enclosed (Experiments 6 and 7) as compared with whole-crown enclosure (Experiment 6), and the relatively low cumulative K efflux during the 5 days of

upper-chamber enclosure in Experiment 7, may possibly be due to some $O_2$ transport from the upper stem, i.e., unenclosed stem portions >25 cm above the root crown. Large elongate lenticels on the basal parts of stem and taproot in the peat-pearlite medium presumably are the primary points of $O_2$ entry, however, as indicated for lodgepole pine (Pinus contorta Douglas ex Louden) by Phillpson and Coutts (1978, 1980).

Anatomic Modifications in Conditioned Roots

During the initial 23 month period in unstirred $CaCl_2$ solutions, root and microbial respiration reduced $O_2$ levels from the air-saturation values of about 11.3 and 7.7 ppm $O_2$ expected at 10 and 30 C, respectively, to a winter average of 4.5 ppm $O_2$ when temperatures were 10 to 20 C, and a summer average of 1 ppm $O_2$ when temperatures were 25 to 30 C. It is not known whether the further five-month period of stringent $O_2$ exclusion preceding the experiments (Table 4-1) was essential to the results obtained. In three other pine species studied (lodgepole pine, Coutts, 1982; Coutts and Philipson, 1978; Philipson and Coutts, 1978; loblolly pine and pond pine, Topa and McLeod, 1986b; McKevlin et al., 1987), growth of roots in $O_2$-depleted media brought about localized hypertrophy of lenticels on the stem, taproot and lateral roots near the air-water interface, and produced longitudinally continuous, gas-filled lacunae within the pericycle of primary roots.

In pre-conditioned slash pine, intercellular spaces occurred within the stele of the 0- (triarch) and 1- (diarch) order root tips. About 5 mm from the root apex, small spaces appeared singly or in clusters between the primary xylem poles, external to primary phloem, apparently as result of cell lysis or rupture. Further from the apex, the spaces merged into lacunae that occupied 50% or more of the stele. At about 15 mm from the apex, where a complete cambium had formed, the growth of secondary vascular tissue had compressed lacunae into a thin peripheral zone.

Such air-space development was not observed in hand-sections of the long 'air-root' tips first grown in aerated solution (Experiment 4), and then subjected to continuous $N_2$ sparging (Experiment 5) Furthermore, these 'air-tips' did not maintain the appearance of aerobic function in micro-aerobic solutions Elongation ceased and a large solute efflux was indicated by both their loss of turgidity and the sudden increase of K levels in the bathing solutions. Presumably the high $O_2$-demand of actively growing root tips (Coutts and Philipson, 1978) and a lack of internal air-conducting space induced the anoxic responses. Although the root systems as a whole regained net uptake of K from the micro-aerobic solutions (within 24 h of return to $N_2$ sparging), the 'air-tips' remained limp and discolored.

Morphology of Conditioned Root Systems

In Chapter 2, we demonstrated a continuous pathway for $O_2$ diffusion in the secondary xylem of large-diameter slash

pine roots. The present study indicates that $O_2$ entering the stem and basal taproot reaches the lower root system in sufficient amount to maintain viable roots, water absorption, and active uptake of K under micro-aerobic conditions. The limited $O_2$ supply, however, seems to impose a characteristic morphology. Root elongation is slow and restricted in length, as compared with the long, less-branched roots that develop very rapidly in air-sparged solutions (Experiment 4). The 0- and 1-order roots are thick but taper rapidly over their relatively short lengths. Diameters of the many 1-order branches are much smaller than the diameters of 0-order mother root, and suggest an efficient configuration for $O_2$ supply. Available $O_2$ is thus distributed to a large number of short 2- and 3-order absorbing roots (Figure 4-2).

Uptake from Saturated Forest Soils

The maximum hourly uptake of K from micro-aerobic solutions, 0.1 to 0.3 nmol K $cm^{-1}$ $h^{-1}$ for roots <1 mm diameter, is small relative to K-uptake rates for roots in aerobic solutions (slash pine, Shoulders and Kaiston, 1975; corn, Claassen and Barber, 1974; plum, Rogers and Carlson, 1954). Nonetheless, absorption by slash pine roots from saturated anoxic soil has the potential for minimizing deep leaching of this mobile element. Pre-conditioned root systems absorbed K from micro-aerobic solutions even more dilute than soil solutions of flatwoods soils (about 20 μM K Blaskerk and Koshnak, 1954) at rates substantially greater

than can be attributed to the mass influx of water (Table 4-2, Figure 4-6).

# CHAPTER 5
# OVERALL SUMMARY

The taproots and associated vertical sinkers of large slash pine trees extend into soil that is continuously saturated and anoxic for months and years at a time. An internal transport mechanism must be capable of conducting $O_2$ over long distances through large-diameter roots consisting almost entirely of secondary xylem. In addressing the general hypothesis that deep woody roots of slash pine are internally aerated, the first study demonstrated an open pathway for $O_2$ diffusion through the wood of slash pine sinker roots (Chapter 2), the second study revealed evidence of $O_2$ leakage from submerged roots into otherwise anaerobic soils (Chapter 3), and the last study showed that internal $O_2$ transport to submerged roots in micro-aerobic environments can maintain aerobic uptake functions (Chapter 4).

Air Conducting Porosity in Green Root Wood

Green sinker roots from the central root systems of two large slash pines growing on a wet soil, and a taproot and sinker root of another slash pine growing on a moderately well-drained soil, were used to determine volumes of wood substance, water and air, and to measure air permeability

Green root wood had a much higher proportion of air-filled pore space than found in other conifers that have been examined, excepting Taxodium. This was the consequence of low root bulk density and low water-filled volume. The large air-filled pore space, 48 to 69% vv, must be confined to the lumina of axial tracheids because intercellular space in secondary xylem is rare and axial tracheids comprise a major part of the axial system. For normal xylem conduction of water to occur, much of the free water must be in connected water-filled tracheids. Likewise, air-filled tracheids would provide a connected network through which either mass flow or diffusion of $O_2$ could occur.

Small pressure gradients forced air through roots up to 40 cm in length. Linear relationships between pressure gradient and outflow allowed the use of Darcy K to characterize air permeability. The K values obtained for roots, mostly between 50 and 90 $cm^2\ kPa^{-1}\ min^{-1}$, were comparable to the air conduction through single capillary tubes less than 1 mm in diameter, or about 0.02% of the root cross-sectional areas. Air flow was generally related to root cross-sectional area, indicating that the air conduction was the result of combined flow through many very small pores, interconnected tracheids, distributed throughout the root cross-section.

The general independence of Darcy K and root length indicated a continuity of air-filled pores through roots at least 40 cm in length. Such continuity favors long-distance

gas transport through sinker wood. Gas diffusion, presumed to be the main mechanism for $O_2$ transport, would occur through the same interconnected pore space that was available to mass air flow. Preliminary experiments showed that air conduction through secondary phloem and the rhytidome was negligible. Thus, the large proportion of air-filled space in green sinker wood and the non-tortuous path offered by interconnected air-filled axial tracheids would enable rapid diffusion from xylem adjacent to lenticels to deep root tips over the range of, perhaps, 1 to 5 m.

Even greater air-filled porosity and greater longitudinal air permeability was observed in large- and small-diameter roots of pond cypress. These roots were extracted from soil at the margin and within normally ponded depressions, and from below the bottom of a lake margin

Iron Oxide Precipitation on Submerged Roots of Slash Pine

The availability of a gas-transport pathway through large woody roots is demonstrated by evidence of Fe oxide precipitation on surfaces of roots growing in saturated anaerobic soil and peat (Chapter 3)

Iron oxide precipitation on roots was observed in two studies, one of slash pine saplings growing in saturated peat (Study I), and the other of central root systems of the two large slash pines described in Chapter 2 (Study II). For the sapling taproots, the distal two-thirds of vertical root extent, about 29 cm in length, survived at least 18 mo

in saturated anaerobic peat. Central sinker roots of the large slash pines extended to 150 cm depth from the soil surface, of which about 95 cm was in subsoil subject to prolonged periods of anoxia.

Iron oxides coated the distal tips of taproots, sinkers, and fine root branches of peat-grown saplings (Study I). The precipitates were located on external root surfaces and on cells in the cortical and epidermal tissues. Large-diameter sinkers and fine lateral root branches of the slash pine trees were also coated with Fe oxides (Study II). Rinds of Fe oxide-cemented soil encased the fine roots and were attached to large-root surfaces in localized patches, from the basal ends of sinkers to the deep distal tips. Iron oxides also coated deep roots of cypress. In each study the localized concentrations of Fe were much higher than in the surrounding matrix.

Reduced conditions dominated the matrix in both studies, as evident from the lack of rust on steel rods and low Eh levels in the saturated-peat matrix (Study I), and ortho-phenanthroline dye reactions with water-soluble Fe(II) in the mineral subsoil matrix (Study II). The precipitation of Fe oxides indicated Fe(II) oxidation at root surfaces, either by direct reaction with $O_2$ released from roots, or by microbial oxidation. Thus, the localized concentration of Fe expressed on the basis of surface area of the associated root served as an index of cumulative radial $O_2$ flux from roots.

Long-distance transport of $O_2$, a minimum of 100 cm from soil surface to the deepest root tips (Study II), must have sustained the viability of the deep roots and supplied the $O_2$ that roots evidently released into the rhizosphere for Fe oxidation. The internal transport mechanism, through air-filled spaces in the wood, effectively aerates the most distal root tips of large diameter sinkers where thick Fe oxide rinds formed. Furthermore, the xylem evidently allowed radial $O_2$ diffusion to the periderm of large woody roots and movement into branch roots. Non-uniform $O_2$ release from large-diameter roots, indicated by patchy Fe oxide precipitation, suggested that $O_2$ leaked through the intercellular space around branch roots or through other breaks in the rhytidome. By analogy, the $O_2$ transported to the distal taproot tips of slash pine saplings (Study I) would also have been through secondary xylem, although root wood properties indicated that the facility for air conduction was not as well developed as in the sinker root wood of large slash pines.

Active K-Uptake from Micro-Aerobic Solutions

The internal transport of $O_2$ to submerged roots was further supported by evidence that K absorption from micro-aerobic solutions depended on the longitudinal transport of $O_2$ from basal portions of the sapling stem or taproot (Chapter 4).

Taproot systems of slash pine saplings were cultured in vertically divided chambers; the basal taproot and lateral

grew in a drained peat-pearlite mixture in the upper chamber, and the lower taproot-sinker root system grew in solutions with restricted aeration in the lower chamber. Grown in this manner for 2 y, saplings then maintained healthy taproot systems for 5 mo in bathing solutions continuously sparged with $N_2$. Oxygen was thus depleted to micro-aerobic levels, about 0.5 ppm $O_2$.

The taproot systems absorbed added K from micro-aerobic solutions, reducing the K concentrations from about 50 μM to steady-state levels of 2 μM in repeated experiments. Fine roots of the same taproot systems maintained high tissue K concentrations, thus indicating that K-uptake was an active, i.e., aerobic, process. Furthermore, the average K-uptake rates were generally greater than could be accounted for by mass influx of K with absorbed water, a passive process.

Internal aeration, which presumably maintained the active uptake of K from micro-aerobic solutions, could not support the same level of aerobic activity that external aeration sustained. Change of the sparging gas from $N_2$ to air initiated new growth from apical meristems and eventually increased the rates of K uptake. Air sparging did not affect the minimum steady state K concentration achieved. The electro-chemical balance between roots and air-sparged solutions was disrupted, however, when $N_2$-sparging resumed. This was indicated by a temporary, but large, net efflux of K from the roots. The new roots then established another, presumably lower, level of activity in

micro-aerobic solution, with net K-uptake by the whole root systems resuming within a day of the change to $N_2$-sparging.

The dependence of active K-uptake on internally transported $O_2$ was shown in experiments that temporarily enclosed the seedling crown and/or the lower stem and upper root chamber in $N_2$-flushed bags, while micro-aerobic conditions were maintained in the lower-chamber solution. Such treatment caused almost immediate net efflux of K from the lower taproot systems, previously at steady state with 2 uM K solutions. The effects of treatment were reversible inasmuch as net K-uptake resumed when enclosures were removed.

The rapid treatment effect and a similarly rapid reversal indicated that K-efflux occurred in immediate response to $O_2$ deprivation in the lower root system, caused when internal $O_2$ transport was reduced. The $O_2$ that was transported down to the roots evidently entered the tree through large lenticels on the basal stem or taproot. The diffusion path from lenticels to root tips obviously passed through stem and roots with advanced secondary thickening; the taproots were 3 to 4 cm in diameter at the bottom of the upper chamber, and were 30 to 40 cm in length from there to within about a centimeter of the root apex. The findings in Chapter 2 indicate that $O_2$ was transported through connected air-filled space in root wood.

Primary tissue structure occurred from the apices of 0- and 1-order roots to within 1 or 2 cm of the apical tips;

The aeration of these tips was probably facilitated by the longitudinally continuous lacunae within the primary stele. Similar structures were observed in the 0- and 1-order root tips of taproots grown in saturated peat (Chapter 3), roots in which Fe oxide precipitation also occurred. Although not examined in either Study I or II, the lacunate stele structure might also be expected in higher-order roots. Formation of the lacunate stele was presumably an adaptive response to inadequate aeration of the rooting medium, since the roots grown in air-sparged solutions lacked lacunae (Chapter 4).

Central Root System Morphology

The large slash pines growing on a pond margin (Chapter 2) had central root systems comprised of a massive taproot, gradually tapering vertical sinker roots arising at various points along the taproot, and other sinkers that descended from major laterals near their juncture with the taproot. The sapling taproot systems, developed in saturated peat (Chapter 3) and in poorly aerated solutions (Chapter 4), might be described, as having thick "carrotlike" taproots and blunt "spear-like" sinkers, with bushy proliferation of short, small diameter, diarch branches

The thick cross-sectional dimensions and relatively short lengths of roots examined in these studies suggest a morphology constrained by longitudinal $O_2$ supply. The dual functions of xylem, that of $O_2$ conduction downwards and water and nutrient conduction upwards (Chapter 2), have

posed conflicting demands that, for slash pine, have resulted in the observed dimensions and configuration. The large xylem cross-section increases the capacity for gaseous exchange, while the short densely branching morphology provides a relatively large, though confined, surface area of small absorbing roots in the saturated zone, with relatively short distances for $O_2$ transport from the woody sinker to the primary root tips.

The localized branching at the deep ends of slash pine sinkers is sufficient to guarantee absorption of free water from saturated or near saturated soil. This capacity would be significant to the tree during periodic drought when surface water is unavailable but might also supply evaporative demand during periods of surface soil saturation, when the extensive but intolerant surface root system is inundated. Plant water stress is a common first response to sudden flooding of unadapted root systems.

The uptake of nutrients from subsoil might be limited by low absorbing-root surface area. Nonetheless, slash pine taproot systems actively absorbed nutrients at concentrations as dilute as soil solutions (Chapter 4) and, thus, might compensate for deep leaching losses or enable utilization of subsoil P.

Hence, slash pine is particularly suited to marginal soil environments between wet soil with prolonged surface ponding and well-drained soil with the phreatic zone greater than 2 m below the surface. The morphological response of

the central taproot-sinker system to water-table depths and fluctuation, and probable physiological or anatomical adaptation with respect to xylem transport of $O_2$, provide a deep, aerated root system with normal absorption and storage functions in saturated anoxic soil.

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## BIOGRAPHICAL SKETCH

Helen M Fisher was born to Australian parents in Port Moresby, Papua New Guinea (now Papua Niugini), in 1953. After only a short residence there, she grew up in tropical, sub-tropical and temperate parts of eastern Australia. Most of her high school years were spent in a suburb of Melbourne, Victoria. She graduated from high school in 1972 and attended Monash University for three years, specializing in chemistry and biochemistry.

An average student, prone to distraction, she looked for adventure away from home, joining the Australian Volunteers Abroad Program in 1975 as a volunteer school teacher in Papua Niugini. It was an enlightening experience for her if not her students for whom atomic theory was as unreal as fractions. There she "discovered" soil science, while growing sweet potatoes in coral sand.

Helen Fisher began a lengthy "career" as a graduate student in 1976 in the School of Agriculture and Forestry, University of Melbourne. There she was employed as the laboratory technician for the Soil Science Section while earning a master's degree in agriculture.

Guided by a committee member in forestry, she explored opportunities to study forest soils in North America. It

was her fortune to be offered an assistantship in the Soil Science Department, University of Florida, resulting in the research reported in the present dissertation.

Helen Fisher left Florida in the spring of 1987, and at the present time, she resides in Idaho with her husband and son where she intends to resume working as a soil scientist.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

E. L. Stone

E. L. Stone, Chairman
Professor of Soil Science

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

R. S. Mansell

R. S. Mansell
Professor of Soil Science

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy

W. G. Harris

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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T. W. Lucansky
Associate Professor of Botany

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate School and was accepted as partial fulfillment of the requirement for the degree of Doctor of Philosophy.

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